WOLF-PREY DYNAMICS AND MANAGEMENT
— PROCEEDINGS —

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Province of British Columbia
Ministry of Environment

WOLF - PREY DYNAMICS AND MANAGEMENT

Proceedings of a symposium held
May 10 & 11, 1988
in
Room 166, MacMillan Building
University of British Columbia
Vancouver, B.C.

Sponsored by:
British Columbia Ministry of Environment, Wildlife Branch
Faculty of Forestry, University of British Columbia
and
Northwest Wildlife Preservation Society

Wildlife Working Report No. WR-40

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PREFACE

The purpose of this symposium was to exchange information about wolf - prey dynamics and wolf management. The need for the symposium was apparent from the large amount of public controversy surrounding wolf control programs in British Columbia. The symposium was sponsored by the B.C. Ministry of Environment, Wildlife Branch; the University of British Columbia, Faculty of Forestry; and, Northwest Wildlife Preservation Society.

Invited papers were presented by researchers of wolf/prey dynamics, wildlife biologists responsible for wolf management programs and others concerned about current wolf management activities. The first day of the symposium addressed biological studies of wolf - prey dynamics, especially those conducted in British Columbia. The second day dealt with differing perspectives on wolf management. Papers presented in these proceedings have not been peer reviewed.

Organizing Committee

Dale Seip, University of British Columbia
Sherry Pettigrew, Northwest Wildlife Preservation Society
Ralph Archibald, Ministry of Environment, Wildlife Branch

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AN INTRODUCTION TO PREDATOR-PREY INTERACTIONS

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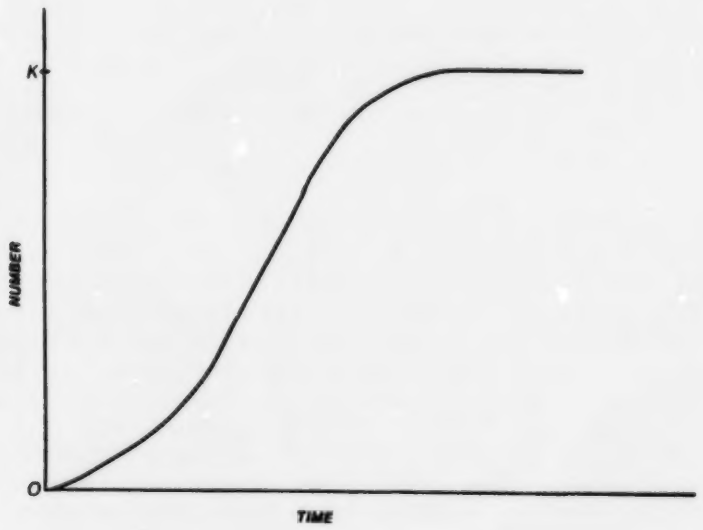
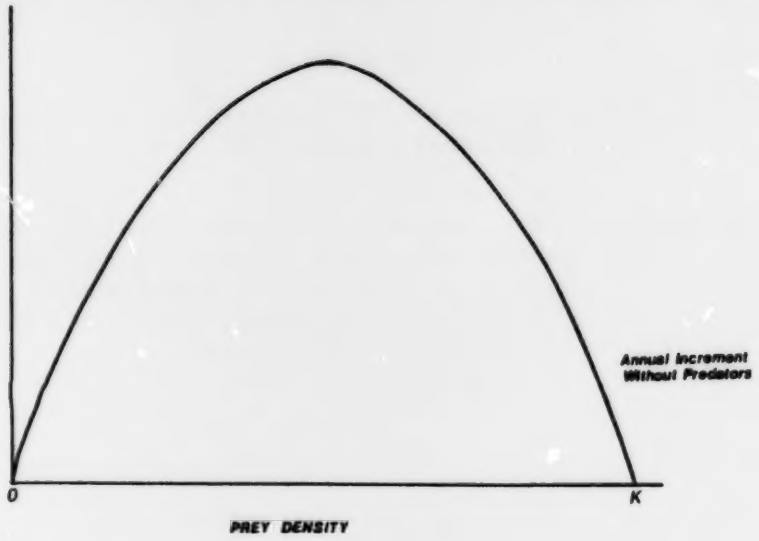
In the absence of predators, prey populations will be regulated by other density-dependent limiting factors such as competition for food or transmission of disease and parasites. These limiting factors will set an upper limit or carrying capacity (K) for the population (Fig. 1).

Figure 1.



The annual increment curve for this typical population growth pattern is a dome shaped curve (Fig. 2). Annual increment is the number of animals that are added to the population each year at different population densities. The annual increment is small at low populations because despite a high population growth rate, the number of reproducing animals is small. At high population numbers, near the carrying capacity, the annual increment is also small because despite the abundance of animals, the growth rate is close to zero due to the density-dependent effects of the limiting factors. The maximum annual increment occurs at an intermediate population where there is a substantial breeding population and the effect of the limiting factors is still moderate.

Figure 2.

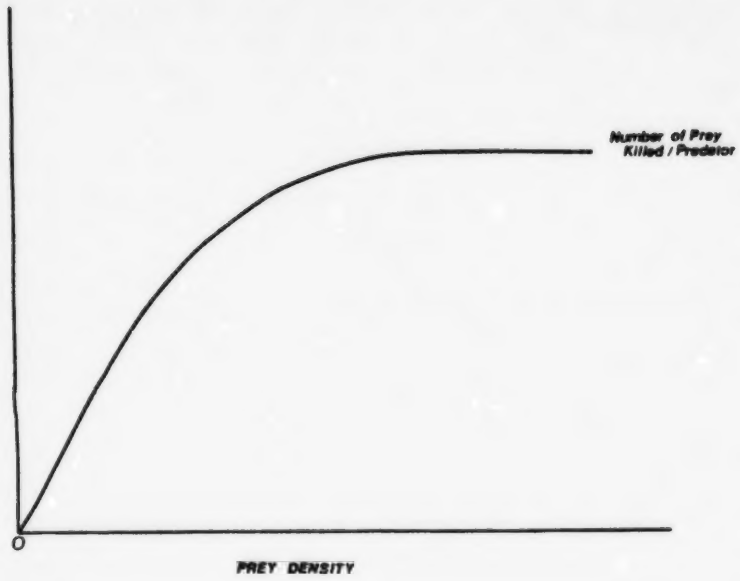


Addition of predators to this system will remove some proportion of the prey population and thereby reduce both the annual increment and the natural equilibrium population. In this paper, I will explain the potential effects of predation on prey populations by removing the number of prey killed by predators from the annual increment that would be produced in the absence of predators. If the number killed by predators is less than the annual increment, the population will increase. If the number killed by predators is greater than the annual increment, the population will decline. The prey population will stabilize at any point where the number killed by predators is equal to the annual increment.

COMPONENTS OF THE PREDATION RATE

The number of prey killed by predators will be the product of the number of prey killed/predator times the number of predators. At low prey densities, the number of prey killed/predator will be small because prey are difficult to find. (Fig. 3). The number of prey killed/predator will increase as the prey density increases and prey become easier to find. However, the prey killed/predator will level off as each predator approaches its satiation point. This general relationship is called the functional response of predators to prey.

Figure 3.



In general, the number of predators will also increase in response to an increase in prey numbers (line a, Fig. 4). This relationship is called the numerical response of predators to prey. However, various modifications of this general relationship are possible. The predator population may level off at an upper population size despite increasing prey numbers due to other limiting factors such as territoriality, disease or lack of other prey species (line b, Fig. 4). In other predator-prey systems, the number of predators may not decline when the prey population declines because the predators have alternate sources of prey to sustain their populations (line c, Fig. 4).

The predation rate (proportion of the prey population killed by predators) will be a function of both the functional response and the numerical response of the predators (Fig. 5). In general, as the prey population increases, the predation rate will increase due to the multiplicative effect of the increasing functional and numerical responses. Therefore, the predation rate is often density-dependent at low prey numbers (ie. the rate of predation increases with increasing prey density). However, the predation rate will become constant (density-independent) if either the functional response or the numerical response level off at higher prey densities. If both the functional response and numerical response level off at high prey densities, the predation rate will decline with further increases in prey density (depensatory or inversely density-dependent predation rate).

Figure 4.

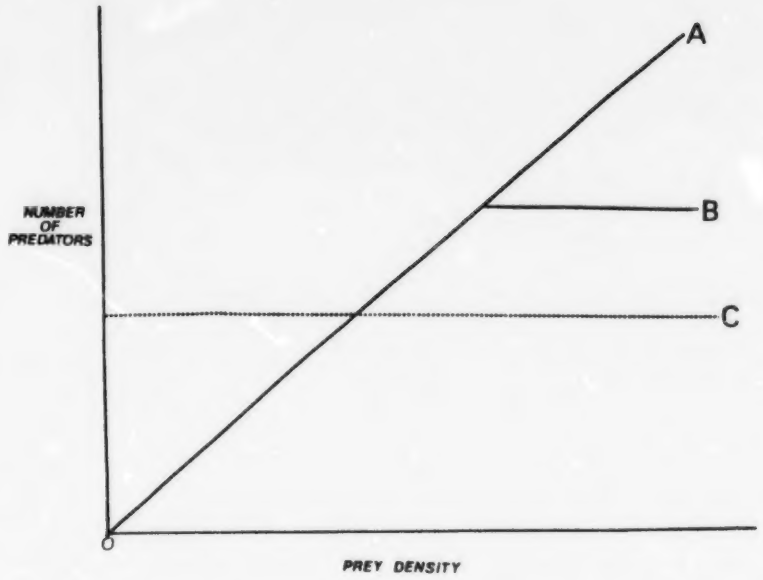
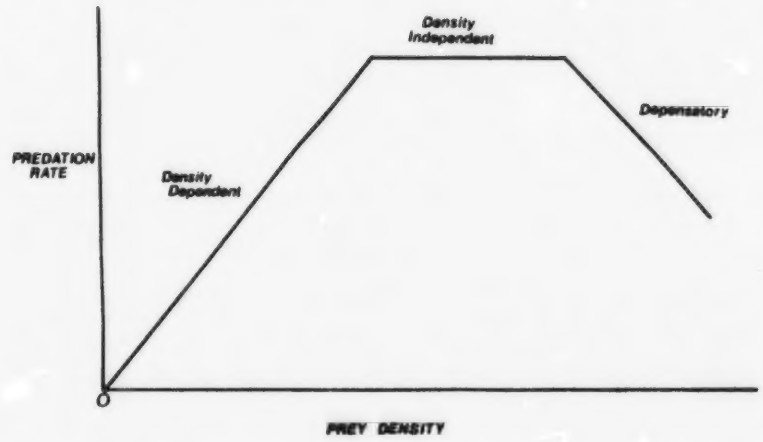


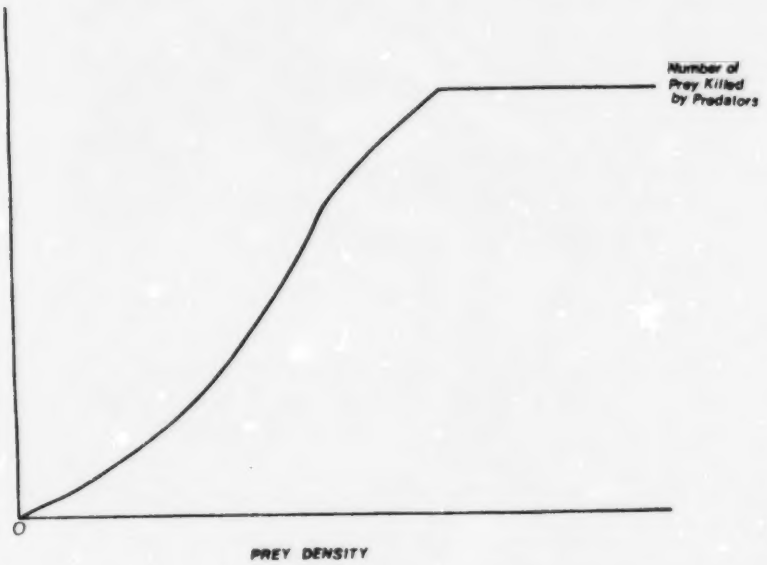
Figure 5.



In terms of the number of prey killed (as opposed to the proportion killed), as the number of prey increase, the number killed by predators will increase exponentially due to the

multiplicative effect of the functional response and the numerical response (Fig. 6). When either the functional or numerical response level off, the number of prey killed will begin to increase linearly with increasing prey numbers. If both the numerical response and functional response level off, the number of prey killed will remain constant with further increases in prey numbers.

Figure 6.

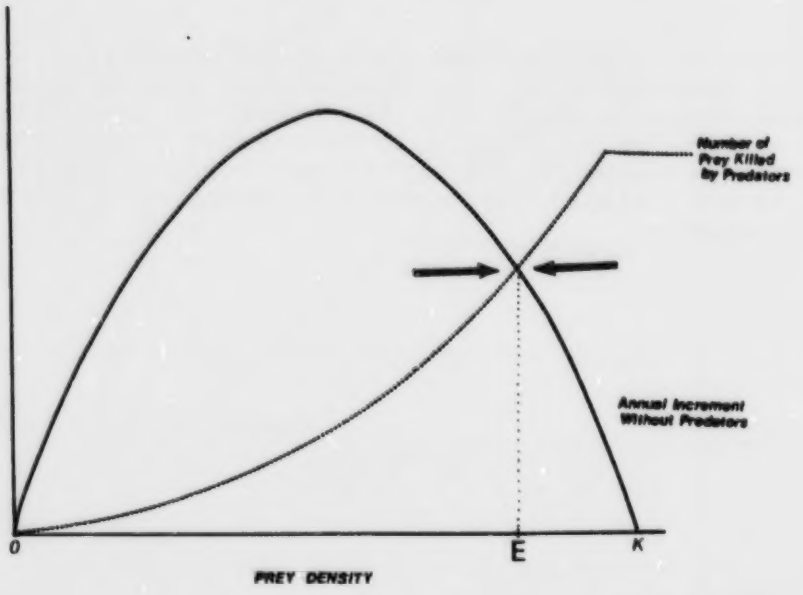


The effect of predation on the prey population can be evaluated by superimposing the graph of number killed by predators (Fig. 6) onto the annual increment curve for the prey population without predation (Fig. 2).

SIMPLE PREDATOR-PREY EQUILIBRIA

If the number of prey killed by predators increases slowly (relative to the annual increment curve) it will intersect the annual increment curve and establish a predator-prey equilibrium at a high prey density (Fig. 7). At prey numbers below the point of intersection, the annual increment of the prey exceeds the number killed by predators and the prey population will increase. At prey numbers above this point, the number killed by predators exceeds the annual increment so the prey population will decline to the equilibrium point.

Figure 7.



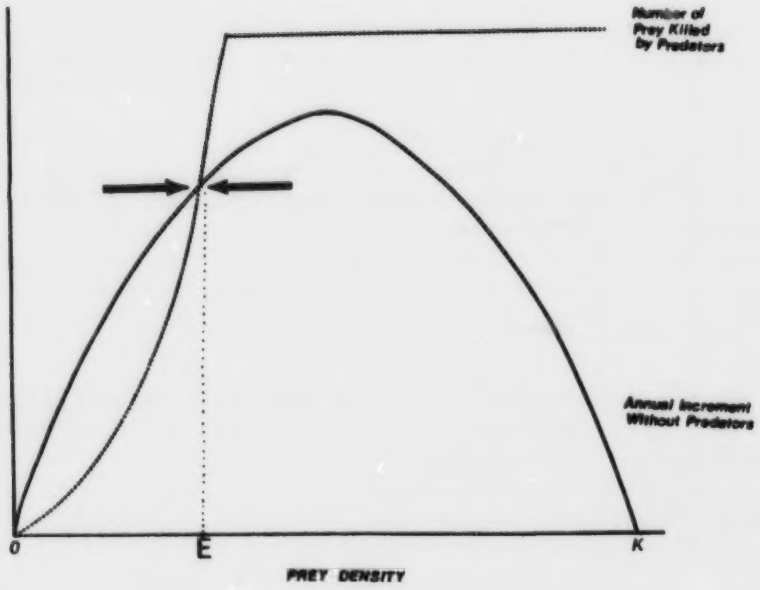
E = Predator-prey Equilibrium

For a predator-prey system of this type, the annual increment and the equilibrium population are not greatly reduced by the predators. This situation will naturally occur when the prey have an effective anti-predator strategy such as use of escape terrain, migrations which lead to spatial separation between predator and prey or the ability to fight off the predator. It will also occur if some limiting factor other than prey availability such as disease, availability of other prey species or wolf control is reducing the numerical response of the predator to the prey. For wildlife populations that naturally exhibit high predator-prey equilibria, there is little justification for predator control because any gains in annual increment or prey populations will be minimal.

If predators are more effective at finding and killing the prey and/or if the number of predators increases rapidly in response to increased prey, the number of prey killed by predators will increase more quickly relative to the annual increment curve (Fig. 8). This situation results in a predator-prey equilibrium at a low prey density, well below the number that could be sustained if predator numbers were reduced.

Low predator-prey equilibria will occur for prey species that do not have effective anti-predator strategies other than living at low densities and thereby making themselves difficult to find.

Figure 8.



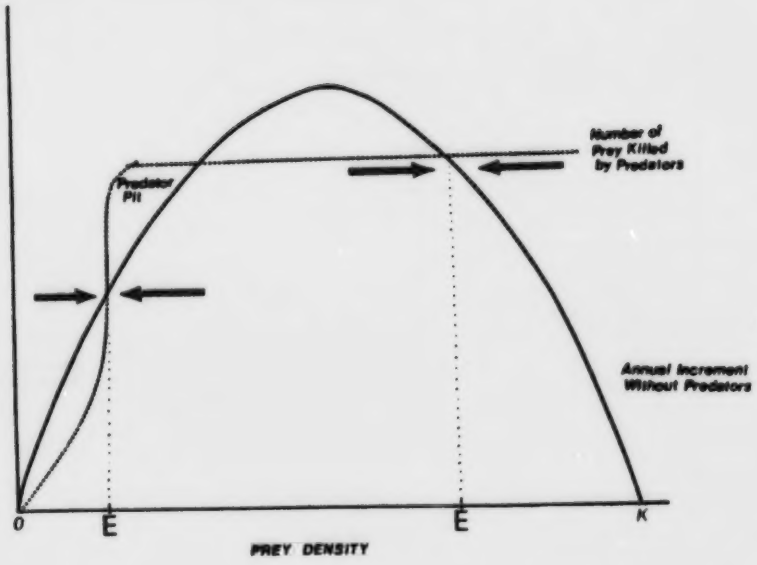
For low predator-prey equilibrium systems, predator control will be an effective means of increasing the prey population. Predator control can be used to reduce the numerical response of the predators and thereby establish a high predator-prey equilibrium as in Figure 7. However, predator control will have to be ongoing because if it is halted, the predators will increase and cause the prey population to decline back to the low equilibrium number.

In reality, the high and low equilibrium systems are points on a continuum. The full range of predator-prey equilibria, ranging from prey extinction to predators having almost no effect, are possible depending on the values for the numerical response, functional response and annual increment curve of the prey. Also, the relationships may change over time or even from year to year due to changes in the environment that affect these relationships. Time lags in predator responses to prey numbers will result in predator-prey cycles around the equilibrium point.

MULTIPLE EQUILIBRIA AND PREDATOR PITS

If the maximum number of prey killed by predators levels off at a number less than the maximum annual increment of the prey population, a multiple equilibrium predator-prey system can occur (Fig. 9).

Figure 9.



This predator-prey system has both a low and a high stable equilibrium point. Between these two points is an unstable equilibrium. Between the lower equilibrium and the unstable equilibrium is a "predator pit", a range of prey numbers where losses to predators exceed the annual increment. Prey populations below the lower equilibrium point will increase because the annual increment exceeds the losses to predators. Prey populations in the range of the predator pit will decline to the lower equilibrium because losses to predators exceed the annual increment. Prey populations between the predator pit and the upper equilibrium will increase to the upper equilibrium because the annual increment exceeds the losses to predators which have now leveled off. Prey populations above the upper equilbrium will decline and stabilize at the upper equilibrium point.

Therefore, if the prey population is low, the predators can keep them at low numbers. However, if the prey population can be increased to a number above the predator pit, the prey population will increase to the higher equilibrium population. Theoretically, predator control could be used to increase a prey population from the low equilibium to a point above the predator

pit and the prey population would then grow to the upper predator-prey equilibrium. Ongoing predator control would not be required because the upper equilibrium is stable.

The prevalence of multi-equilibria predator-prey systems is debatable. Situations that appear to be a single low equilibrium system may actually be the lower equilibrium point of a multi-equilibrium system. Similarly, systems that appear to be a simple high predator-prey equilibrium may crash to a low equilibrium if the prey population is reduced into an unforseen predator pit by hunting, severe weather or other limiting factors.

Multi-equilibrium systems are most likely to occur when the number of predators levels off due to limiting factors other than prey density. However, the only conclusive way to determine if a predator-prey system has several stable equilibria is to manipulate prey numbers and then allow the system to naturally equilibrate.

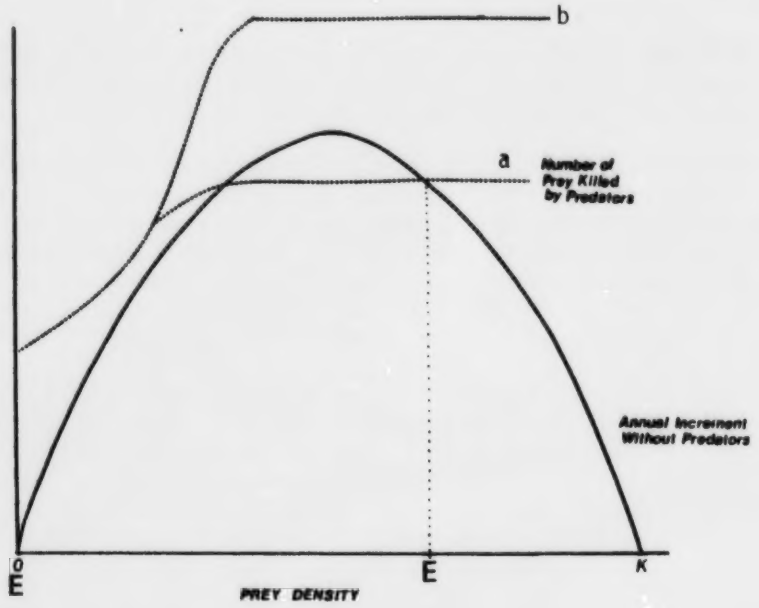
If predator control is to be used to increase a low prey population, the program should be designed to test if the system has a higher predator-prey equilibrium that is stable without ongoing predator control. After the prey population has increased, predator control should be stopped and the prey population monitored. If it is a single low-equilibrium system, the prey population will decline to low numbers and ongoing predator control would be required to maintain higher prey numbers. However, if it is a multi-equilibrium system, the prey population will stabilize at a higher number and ongoing predator control will not be necessary.

PREDATOR PITS AND PREY EXTINCTIONS

If a predator population is sustained by several prey species, the number of predators and the predation rate may be maintained at levels that are sufficient to exterminate one or more of the prey species. Even though some of the prey species are declining to extinction, the predator numbers are sustained by the alternate prey species. The number killed by predators can exceed the annual increment of some of the prey species all the way to the point of extinction. This predator pit may be part of a predator-prey system that has a stable equilibrium at higher prey densities (line a, Fig. 10) or alternatively there may be no stable equilibrium in the system for that prey species (line b, Fig. 10).

The latter case will rarely be observed because the prey species will soon be extinct. However, the prey may be observed in the process of going extinct if the conditions leading to this

Figure 10.



situation have only recently been established by environmental changes such as colonization by a new alternate prey species. If the system does have a stable predator-prey equilibrium at higher prey densities, the existance of this predator pit may remain unknown unless the prey population is reduced into the predator pit by other limiting factors such as hunting or severe weather.

If a wildlife population is in a predator pit of this type, predator control is probably required to prevent the prey from going extinct. If the system has a stable equilibrium at higher prey densities, temporary predator control to boost the prey out of the predator pit will suffice. However, if there is no stable equilibrium, ongoing predator control will be required if the prey species is to be saved from extinction in the area.

PREDATION AND HABITAT

Changes in habitat characteristics can alter predator-prey systems in various ways:

1. Removal of escape terrain or escape cover can increase the predation rate resulting in a lower prey population.

2. Reducing the amount of suitable habitat can concentrate the prey into a smaller area leading to a higher predation rate and a reduced prey population.

3. Habitat changes that encourage the establishment or loss of alternate prey species may alter the dynamics of existing predator-prey systems.

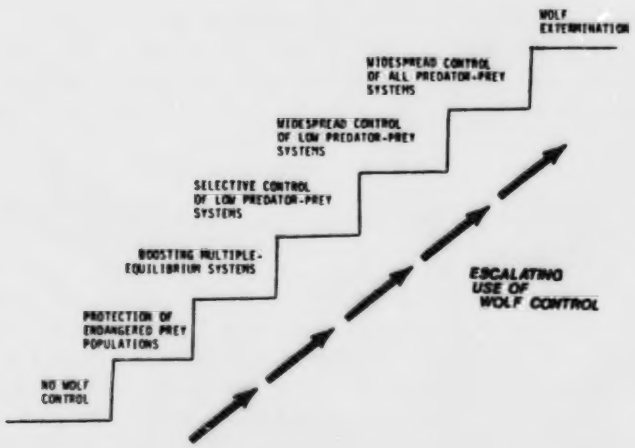
4. Habitat changes that increase or decrease the productivity of prey species will affect the annual increment curve and the ability of the prey to sustain losses to predators.

Therefore, habitat protection and management may be as important as predator control as a means to manage some predator-prey systems.

IMPLICATIONS FOR WOLF CONTROL

The controversy over use of wolf control for wildlife management often becomes polarized as a debate between those for and those against. However, given the variety of possible predator-prey interactions, the question should be "Under what conditions is wolf control justified?". There is a continuum of wolf control applications ranging from no control under any circumstances to extermination of the wolf (Fig. 11).

Figure 11.


WOLF EXTERMINATION
WIDESPREAD CONTROL OF ALL PREDATOR-PREY SYSTEMS
WIDESPREAD CONTROL OF LOW PREDATOR-PREY SYSTEMS
SELECTIVE CONTROL OF LOW PREDATOR-PREY SYSTEMS
BOOSTING MULTIPLE-EQUILIBRIUM SYSTEMS
PROTECTION OF ENDANGERED PREY POPULATIONS
NO WOLF CONTROL
ESCALATING USE OF WOLF CONTROL

Probably very few people support either of these extremes. Intermediate options, ranging from the most conservative to the most liberal application of wolf control for wildlife management, include:

1. Wolf control to protect a prey species from local extinction. This control can be temporary if there is a stable predator-prey balance possible at higher prey numbers. However, wolf control will have to be ongoing if no such stable equilibrium point exists.

2. Wolf control to boost a multi-equilibria system from the low prey equilibrium to the high prey equilibrium. This wolf control can be temporary because once the prey population escapes the predator pit, it can stabilize at the higher predator-prey equilibrium point without ongoing wolf control. Because the prevalence of multi-equilibrium systems is unknown, this application of wolf control should be approached experimentally.

3. Wolf control to increase prey populations that are naturally held at low densities by predators. Reducing the numerical response of the wolves can establish a predator-prey equilibrium at a higher prey density. Ironically, the number of wolves that can be maintained at this higher equilibrium may be greater than what is present at the natural low predator-prey equilibrium. Therefore, it may be possible to use wolf control to actually maintain higher wolf populations in the long term. However, ongoing wolf control is required to maintain this higher equilibrium. If wolf control is stopped, the wolves will increase and reduce the prey population to the lower equilibrium point.

A further management decision associated with this option is whether it is going to be restricted to selected areas that contain high priority prey populations or if its application is going to be wide-spread.

4. Widespread wolf control to increase all prey populations. Since this approach would include areas that have naturally high predator-prey equilibrium systems, the benefits of this approach would be minimal in many areas.

TOWARDS UNDERSTANDING THE RELATIONSHIP BETWEEN WOLF PREDATION AND MOOSE DENSITY IN SOUTHWESTERN QUÉBEC

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Abstract: Moose-wolf interactions were studied in three hardwood-conifer forest areas of southwestern Québec from 1980 to 1984. The three study areas had differing moose densities (0.17, 0.23, and 0.37·km^{-2}) created by human hunting, not by habitat differences. At the lower range of moose densities, wolf predation proved to be density dependent (6 to 19% of the moose population per year) and importantly reduced the population growth rate of moose. The increase in predation rate was not associated with deteriorating foraging conditions for moose. The study lends support to the concept that wolf predation can have an important regulatory effect at low moose densities but also a depensatory (inversely density dependent) effect at higher densities (>0.5-1.0·km^{-2}). Three population models are presented: food, predation, and food-predation. Each population model assumes different mechanisms of regulation that can create potential density equilibria (1 or 2). Wildlife managers wishing to determine the sustainable harvest of moose populations in North America should consider those population models incorporating the density relationship of wolf predation.

Paper presented at the Symposium on wolf-prey dynamics and management, May 10-11, 1988, Vancouver, B.C.

INTRODUCTION

For most ungulate populations, the interaction between natural mortality and population density constitutes the central element of any model of population dynamics (Caughley 1976). Many studies have illustrated changes of mortality and recruitment rates in moose (Alces alces) as a function of nutrition, climate, and predator abundance (Pimlott 1959; Blood 1973; Simkin 1974; Rolley and Keith 1980; Hauge and Keith 1981; Mytton and Keith 1981; Gasaway et al. 1983; Messier and Crête 1984, 1985; Seather and Haagenrud 1985; Franzmann and Schwartz 1985; Albright and Keith 1987). However, comparatively few studies have actually documented the relationship between these limiting factors and density-dependent changes in population parameters (e.g., Crête et al. 1981; Messier and Crête 1985).

In 1977, an intensive research programme on moose population dynamics was initiated in southwestern Québec. The first phase of the programme (1977-1980) was designed to assess moose-habitat and moose-hunter interactions (Crête et al. 1981). The general approach was to study different moose populations inhabiting comparable habitats, but "manipulated" at various densities due to differing hunting regimes (see Macnab 1983 for a comment on "Wildlife management as scientific experimentation"). Specifically, comparisons were made between a population near a natural equilibrium density (i.e., lightly hunted for a few decades) and other populations at lower densities (i.e., more heavily hunted). The research revealed that the sustainable harvest rate decreased markedly from 20-25% to 3-5% per year as moose density increased from ≈0.15 to 0.40 moose·km^{-2} (Crête et al. 1981; Messier and Crête 1984). Therefore, the population growth rate, as evaluated by the sustainable harvest (Caughley 1976), was progressively reduced to nearly zero when moose density approached the density of 0.4·km^{-2}, indicating that some sort of density dependent regulatory mechanism was operating over the examined range of moose densities.

The hypothesis that the population was regulated by food competition was tested. Firstly, there was no indication from examination of four body attributes (Messier and Crête 1984) and several blood parameters (Crête et al. 1982) that foraging conditions deteriorated when a moose population reached 0.4 animal·km^{-2}. Secondly, moose consumed less than 10% of the browse biomass in wintering areas, even in areas of high moose densities (Crête and Jordan 1982a). Thirdly, an enrichment of the shrub strata following an outbreak of the spruce budworm (Choristoneura fumifera, Crête and Jordan 1982b) did not result in higher recruitment rates or an increase in moose density (Messier and Crête 1984). It was, therefore, concluded that the decline in the population growth rate at densities approaching 0.4 moose·km^{-2} was not attributable to nutritional stress.

As an alternative to food regulation, predation by wolves and/or black bears (Ursus americanus) was suggested as a density-dependent population process (Crête et al. 1981). This hypothesis formed the basis of the second phase of the research programme that lasted from 1980 to 1984.

STUDY AREA AND METHODS

Moose-wolf interactions were studied in three adjacent, hardwood-conifer forest areas of southwestern Québec (Fig. 1 of Messier and Crête 1984). Area H, the game reserve La Vérendrye (13,615 km^2), had a relatively high moose density (0.37 animal ·km^{-2}) because of a restricted hunting pressure (3-4% annually). Area M (2,390 km^2) and L (1,185 km^2) had a moderate (0.23·km^{-2}) and a low moose density (0.17·km^{-2}), respectively. These lower densities were caused by intense hunting pressure (20-31%

annually). Density estimates were derived from aerial surveys in January following the hunting season (Crête et al. 1986). Habitat structure and forage production were comparable among the three study areas (Crête and Jordan 1982a), hence they were assumed not to be the causal factor of the differing moose densities among areas.

White-tailed deer (Odocoileus virginianus), the only alternative ungulate species, were rare in the study areas (Fig. 1 of Messier 1985a). Black bear (Ursus americanus) densities were unknown, but tracks and droppings were common in the three study areas; area H likely supported the highest density with a minimum of 0.25 bear·km^{-2} (Lachapelle et al. 1984). No other large predator species was present.

The ecology of wolves was studied using radio telemetry methods from June 1980 to February 1984. Fifty-four wolves from 14 contiguous packs were radio-tracked by airplane. Some 4,700 wolf locations were accumulated during 2,000 hours of flying time. Radio-tracking permitted us to document pack size, wolf densities, and killing rates. Food habits of the wolves were determined from scat analyses in summer (May to November) and aerial observations during telemetry flights in winter (December to April). Moose killing rates were calculated from the number of wolf-days of tracking and the number of kills observed. All observed moose carcasses were ground-investigated, within a few days following discovery, in an effort to differentiate wolf kills from natural deaths (i.e., old age, starvation).

PREDATION RATE

Two types of information were used to evaluate predation rate: wolf density estimates (the numerical response) and killing rate per individual predator (the functional response). Wolf density in January increased with moose density, from 0.36, to 0.82, to 1.38 wolves·100 km^{-2} in areas L, M, and H, respectively (Table 1). Similarly, killing rate in winter increased with moose density from 0.37, to 0.47, to 1.12 moose·100 wolf-days, respectively. In summer, killing rates could not be documented, although scat analyses revealed that moose composed 65%-84% of the biomass ingested by wolves. Based on winter killing rates and moose consumed in summer (see messier and Crête 1985), year-long predation rate was estimated to represent 6.1, 10.7, and 19.3% of the moose population in areas L, M, and H, respectively (Table 1).

Empirical information from the study provided compelling evidence that wolf predation was density-dependent in the lower range of moose densities. Both numerical and functional responses of wolves were implicated in this relationship. At relatively low moose densities (<0.2 moose·km^{-2}), wolves were

Table 1. Summary of data relative to wolf predation on moose in three areas of southwestern Québec (Messier and Crête 1985)

	Area L	Area M	Area H
Moose density (No./km^2)	0.17	0.23	0.37
Wolf density (No./100 km^2)	0.36	0.82	1.38
Killing rate (No./100 wolf-days)	0.37	0.47	1.12
Percent moose biomass in wolf diet during summer period	67	67	86
Food intake rate in summer (Kg/wolf/day)	2.1	2.2	2.6
Year-long predation rate (% postnatal population)	6.1	10.7	19.3

nutritionally stressed and their density remained low due to poor survival and reproduction (Messier 1985b, 1987). When moose density increased above this density threshold of 0.2 moose·km^{-2}, wolves could successfully colonize the area, although in their initial struggle to subsist they exploited their prey base intensively. Within the range of moose densities permitting full colonization by wolves (approximately between 0.2 and 0.5 moose·km^{-2}), larger and more numerous packs were present and wolf density increased substantially. Similarly, the importance of moose in wolf diet, and the actual killing rate per predator, increased with moose density, thus exacerbating the effect of a greater abundance of wolves. It was during this colonization phase that wolves exerted their greatest impact on moose populations.

In a more general context, wolf predation cannot always be assumed to be a density-dependent process. At moderate to high moose densities relative to food carrying capacity (>1.0 moose·km^{-2}), the proportion of moose killed in a population may actually decrease for three reasons: 1) social behaviour (territoriality, deferred reproduction) would restrain wolf population growth due to habitat saturation (Packard and Mech 1980), 2) wolves would progressively become food satiated, and 3) subtandard moose individuals would be more available and would likely represent a greater proportion of wolf kills (Peterson et al. 1984). Indeed, Gasaway et al. (1983) reported that wolf predation increases during a moose decline from high densities, suggesting an inverse density-dependent relationship. Overall, then, the rate of wolf predation on moose appears to be characterized by a density-dependent (regulatory) phase at low moose densities and an inverse density-dependent (nonregulatory) phase at moderate-high moose densities (Fig. 1).

POPULATION MODELS

In a predator-free area, a moose population is expected to display logistic growth, resulting in a single, upper density equilibrium (K_1 of Fig. 2), normally referred to as the food carrying capacity (Macnab 1985). Competition for nutritious forage with increasing density would then restrain fecundity and accentuate food-related mortality. The most important prediction of the food population model is that in the absence of human hunting moose must be nutritionally stressed when the rate of population growth approaches zero. Moose populations not subjected to wolf predation frequently reach densities greater than 2 animal·km^{-2} (Bergerud and Manuel 1969; Blood 1973; Mercer and Manuel 1974; Cairn and Telfer 1980; Albright and Keith 1987). In Sweden, for example, high densities (3-4·km^{-2}) were reported in the 1970's and population growth was still in the range of 10-20% per year (Cederlund and Markgren 1987). These density figures do not compare with the upper limit of 0.4 moose·km^{-2} as observed in southwestern Québec.

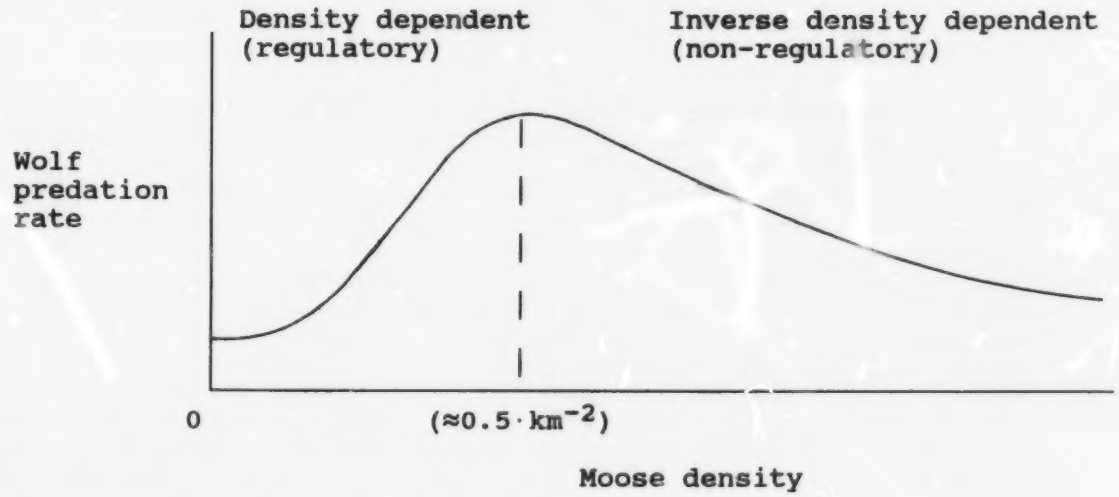

Fig. 1. The hypothesized density relationship of wolf predation across a wide range of moose density in boreal forest.

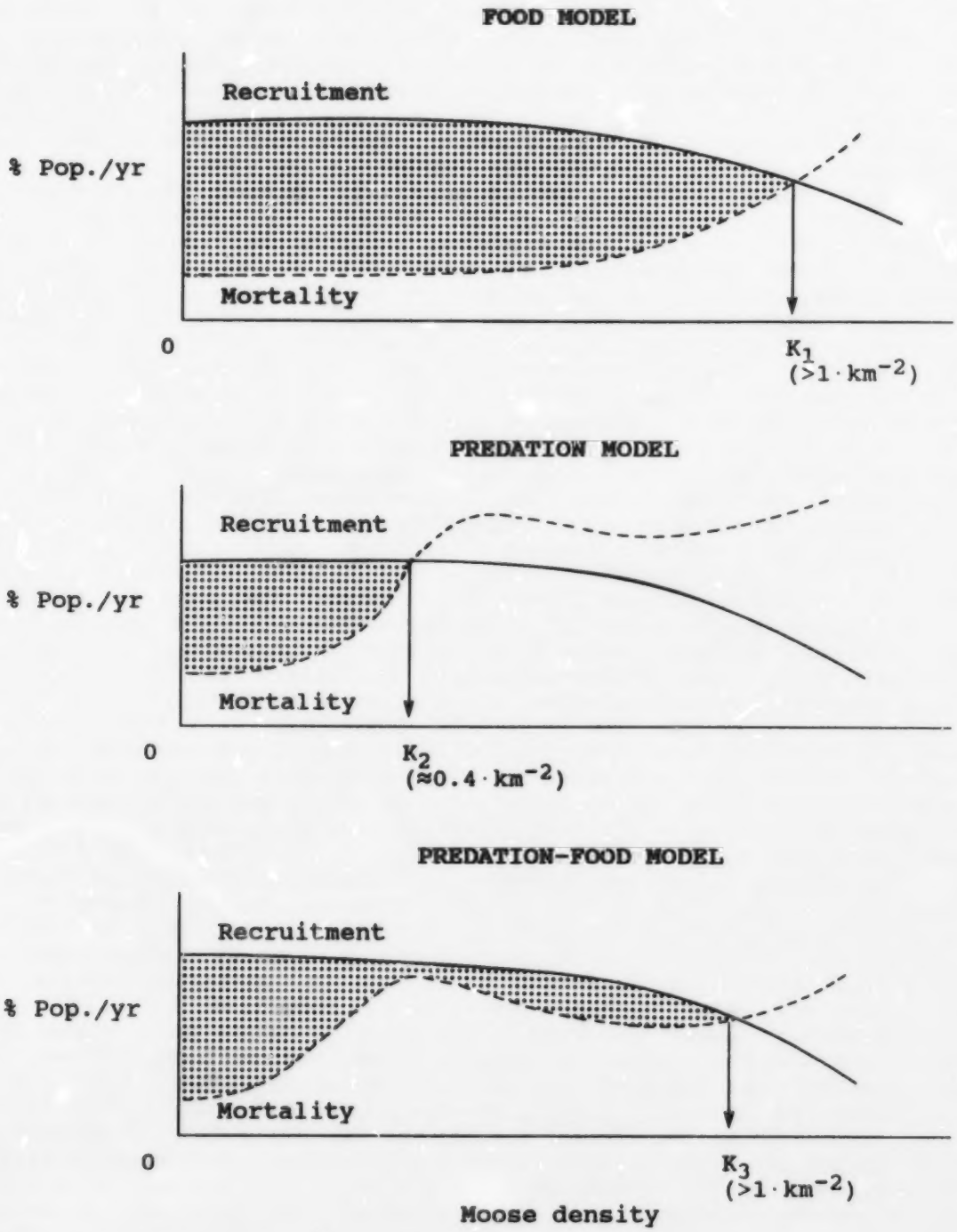

Fig. 2. The three population models described in the text. Shaded areas represent population growth. Mortality is the product of food-related deaths and predation (see Fig.1).

When wolves are present, two types of population models may be relevant. First, predation may severely reduce moose population growth at low densities because of a strong density-dependent relationship. Therefore, moose populations may be forced to stabilize at a relatively low density (K_2 of Fig. 2) and before food competition becomes a major regulatory factor (Messier and Crête 1985; Ballard 1988). Under these conditions, habitat enrichment programmes may have little effects on moose numbers. This population model seems to best explain the situation existing in southwestern Québec (Messier and Crête 1985).

The second type of population model that considers the effects of wolves refers to a situation where predation reduces but does not stop further population growth at low densities. Here, wolf predation reaches a maximum rate at low-moderate moose densities where a positive, yet limited population growth can occur. The moose population will eventually stabilize at high densities due to density dependent food limitations (K_3 of Fig. 2). For example, this population model may best explain the predator-moose-habitat interrelationships at Isle Royale National Park, Michigan. There, moose densities have been fluctuating in a range of 1.0-3.0 moose$\cdot km^{-2}$ with the presence of wolves (Peterson and Page 1983).

Why do wolves appear to be associated with a relatively low density equilibrium of moose in southwestern Québec (and probably in many other places in the boreal forest), but not at Isle Royale? The difference may be linked to the presence of a second predator species, the black bear. Predation by black bears on moose calves has been well documented in Alaska (Franzmann et al. 1980). In southwestern Québec, black bear predation in summer was tentatively estimated at 30% of the annual calf production (Messier and Crête 1985). The density relationship of bear predation is still unknown, although a prediction can be made. Assuming that black bear density is not affected by a greater abundance of moose (because bears rely primarily on a vegetarian diet), and that their killing rate on calves increases linearly with moose density (because of higher probability of encountering calves), then, one would predict a density independent rate of predation. Even if bear predation is constant relative to moose density, the "across the board" reduction in calf production would increase the possibility that a moose population is held a low densities due to density dependent wolf predation. In other words, the lowered recruitment curve relative to bear predation does, in effect, modify the population model from a "predation-food" to a "predation" type (i.e., imagine the predation-food model in Fig. 2 with a lower recruitment curve and envision the change in the equilibrium point).

SUSTAINABLE HARVEST

A primary conclusion to be drawn from the present research programme is that wolf predation drastically changes the relationship between sustainable harvest and moose density, as compared to a situation where predation does not occur (Messier and Crête 1985; Crête 1987). The "yield curve" may no longer have a bell shape as suggested by Caughley (1976) where the harvestable surplus declines to zero at food carrying capacity (Food model, Fig. 3). Rather, the yield curve may be shifted to low moose densities with no possible sustainable harvest above low-moderate densities (Predation model, Fig. 3), or the yield curve may be a complex function with two maxima separated by a range of densities offering little sustainable harvest (Predation-Food model, Fig. 3). In these two latter cases, the harvestable surplus is dictated primarily by the level of predation, not by food limitations. Thus, managers should not assume that the sustainable harvest increases with moose density under adequate habitat conditions.

Another related conclusion to be drawn from this research is that manipulations of moose density by controlled harvest are effective in changing the partition of the annual population increment between natural predators and humans. In southwestern Québec, for example, low levels of hunting in wildlife reserves allows moose populations to reach densities at which wolf predation constitutes the predominant mortality factor. Conversely, moose densities in many hunting zones are kept at lower densities due to more liberal harvest regimes. There, wolf predation rates are much reduced and human exploitation represents the predominant mortality factor. Managers, thus, can take advantage of the decrease of wolf predation when moose densities are maintained at low densities. The maximum sustainable yield in southwestern Québec is achieved when moose densities are kept at 0.2-0.3 moose$\cdot$km^{-2} without active wolf control (Crête et al. 1981, Crête 1987).

A FINAL COMMENT

The three population models presented here are based on different regulatory mechanisms. These models help to conceptualize what sets upper limits to population growth in moose. They are, however, deterministic in nature and describe specifically the basic density relationships of dominant limiting factors. Few studies have shown that fecundity and survival rates of moose are subject to unpredictable perturbations such as winter severity and summer precipitation (Mech et al. 1987; Thompson and Peterson 1988). Although weather conditions, as perturbing factors, undoubtedly generate fluctuations of moose numbers from one year to another, they do not generate density-dependent sources of regulation. Therefore,

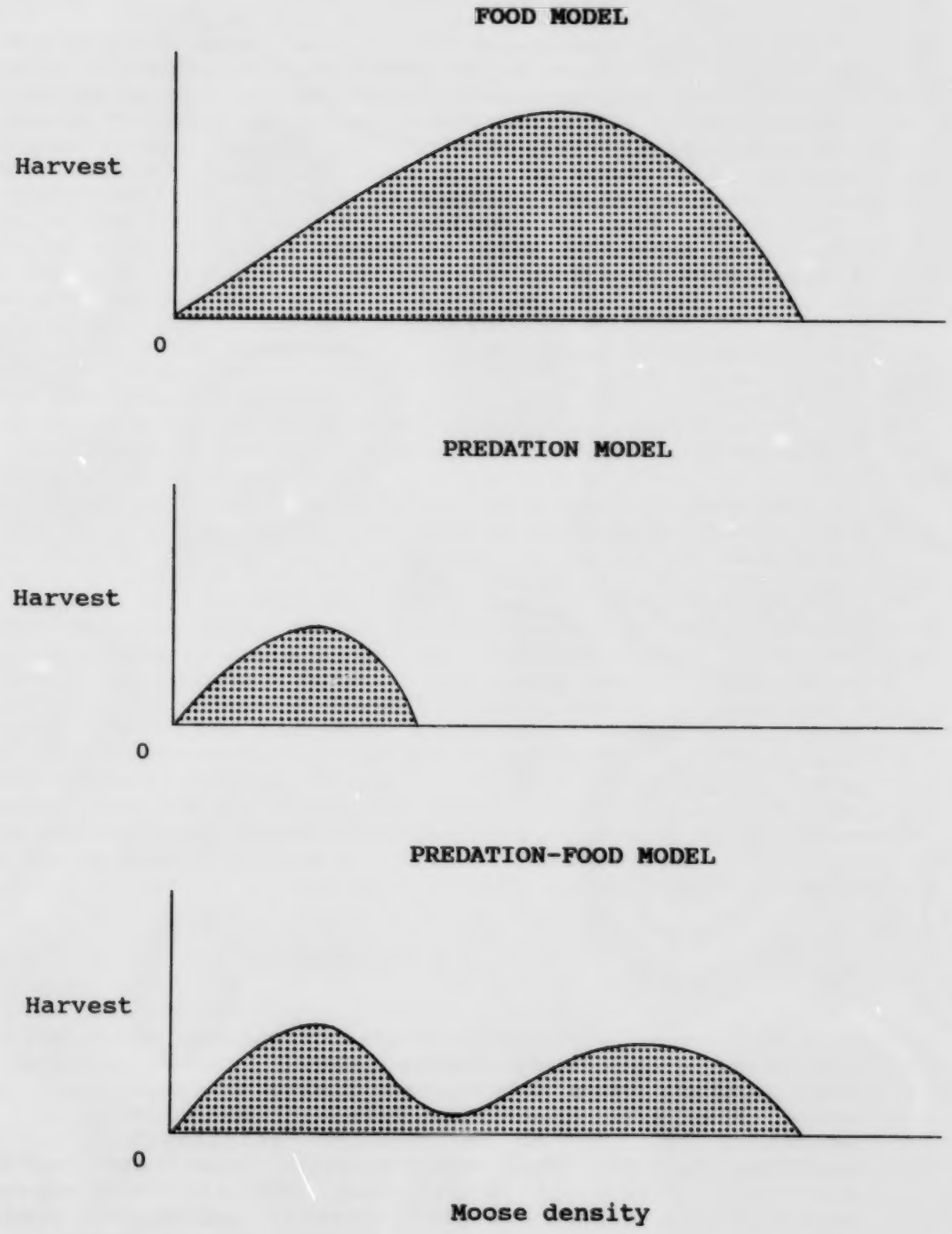

Fig. 3. Changes in the sustainable harvest as a function of moose density according to the three population models presented in Fig. 2.

winter severity, for example, cannot explain basic changes of fecundity and survival rates occurring at different densities; perturbing factors merely help explain the variance of population parameters.

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Wolf-deer interactions on Vancouver Island - A Review

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Scientific knowledge and understanding of wolf biology and predator-prey systems has increased substantially over the past 10 to 15 years. Various factors account for this increase, including a change in public attitudes towards predators (especially wolves), advancements in research technology (telemetry), and a general increase in wolf numbers across temporal North America (e.g. Carbyn 1983). Prior to the repopulation of wolves on Vancouver Island and subsequent documentation of wolf-prey interactions, for example, very little information was available on these relationships in coastal forests.

The purpose of this paper is to review the predator-prey system on Vancouver Island, including information on deer declines, wolf abundance, interactions between wolves and prey, and current management activities. The information and sequence of events is presented in a chronological fashion as encountered by regional wildlife staff.

Deer Declines

Indications of declining deer populations became evident on northern Vancouver Island (specifically in M.U.1-11, Fig.1) in the mid to late seventies. Documented by annual spotlight counts, deer numbers declined by 50 to 75% over the period 1976 to 1981 (Hebert et al. 1982; Jones and Mason 1983; Hatter 1984). Concomitant with the deer declines, hunter harvest also declined substantially, ranging from 23 to 75% within individual M.U.'s on northern Vancouver Island (Fig. 2).

Possible causes for these drastic declines were first related to factors that traditionally received the majority of management emphasis -- deer harvest and habitat requirements, including habitat influence on animal condition. Although there was no previous evidence to indicate that hunting could cause significant declines in black-tailed deer in the coastal environment (e.g. Smith 1968), and hunting regulations during the period of decline were more conservative compared to the late 1960's, hunting was identified as a possible causative factor, especially by the public. Habitat factors, specifically the quality and quantity of old-growth winter ranges and, more generally, the effects of logging practices and succession on deer habitat, were previously regarded as the major determinants of ungulate status on Vancouver Island (Hebert 1979; Bunnell and Jones 1984). Initiated in 1972, the identification and subsequent deferral of deer winter ranges has been a major management activity. By 1974/75, the majority of remaining old-growth winter ranges in the Nimpkish Valley had

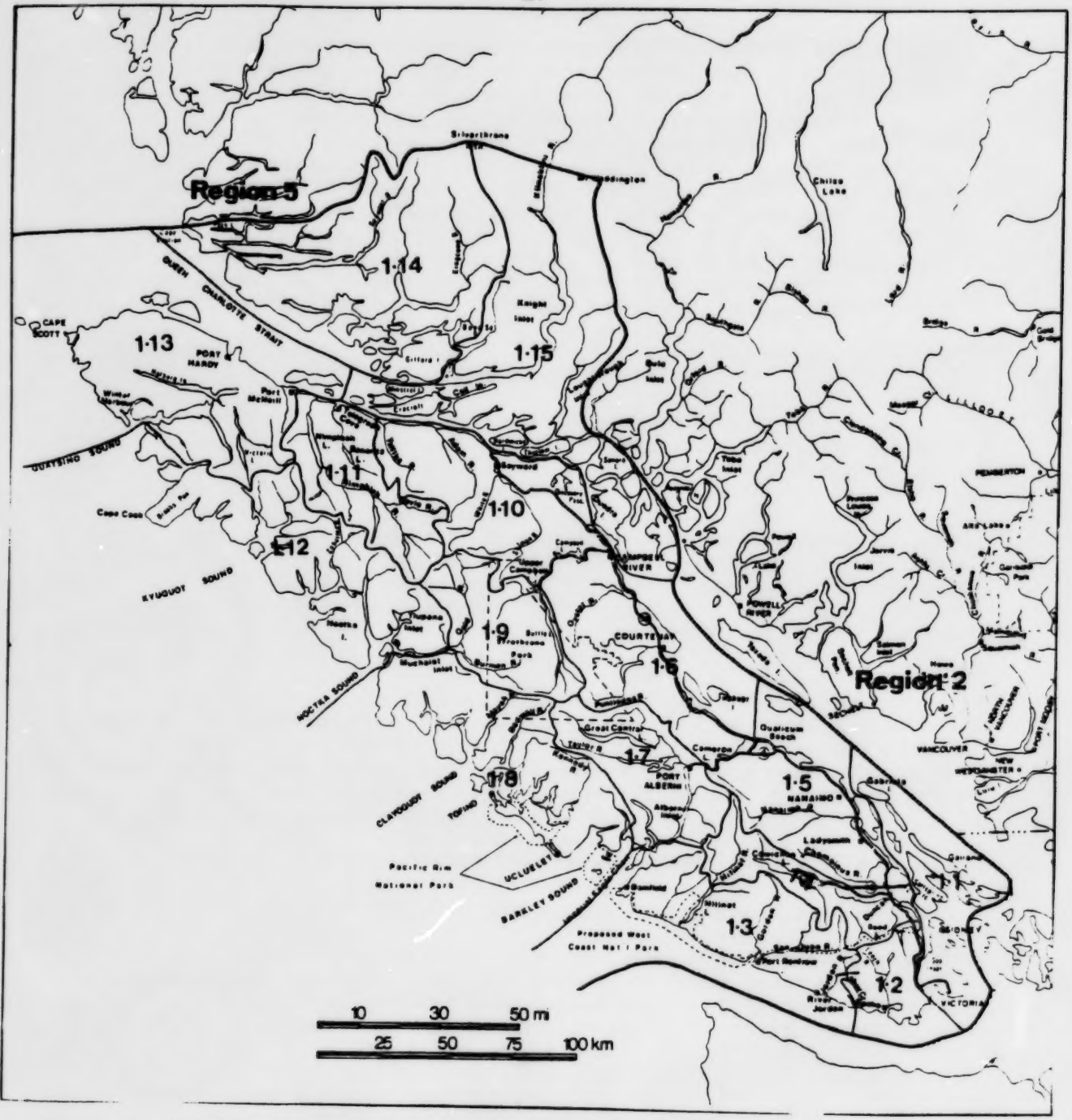

Figure 1. Wildlife management units (M.U.'s) on Vancouver Island. Southern Vancouver Island refers to M.U.'s 1-1 to 1-8 and northern Vancouver Island, from M.U.'s 1-9 to 1-13.

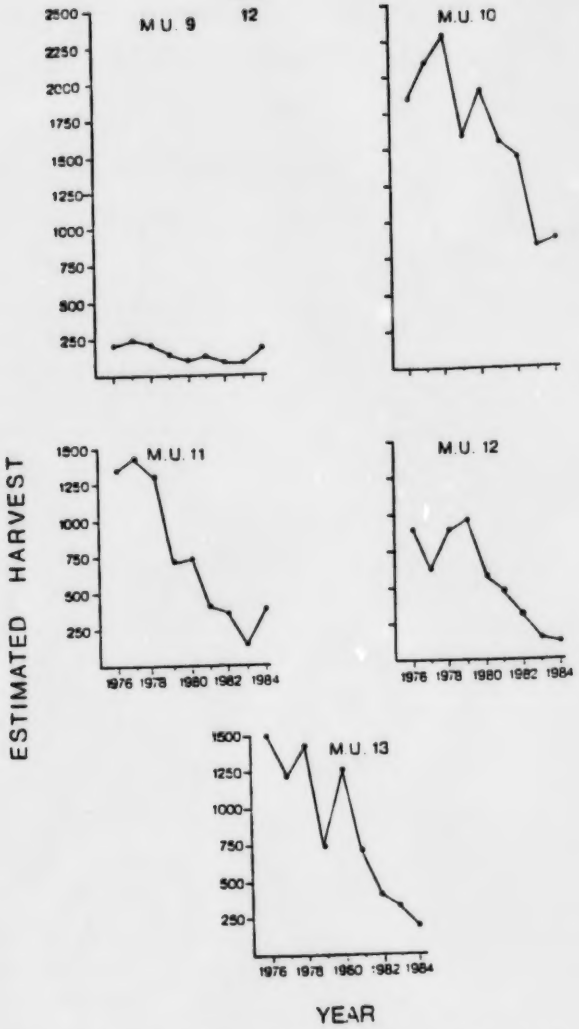

Figure 2. Estimated annual deer harvests for M.U.'s 1-9 to 1-13 (from Janz and Hatter 1986).

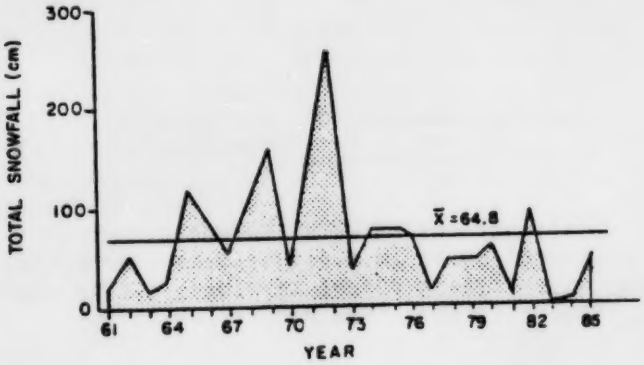

Figure 3. Total annual snowfall recorded at Port Hardy airport (Nov. to Apr.); 61 refers to 1960-61 winter, etc. (from Janz and Hatter 1986).

been deferred from logging (approximately 6000 ha). In addition to availability of high quality deer habitat, winter weather conditions were relatively mild over the period of substantial deer declines (Fig. 3). Further evidence suggesting that habitat and/or hunting were not the limiting factors was revealed by indications of similar declines in deer numbers in undeveloped, inaccessible watersheds (Jones and Mason 1983). Associated with declining deer numbers, however, was evidence of increasing wolf abundance and distribution. The percent of the Nimpkish deer count transects having wolf sign increased substantially during the mid to late seventies, and was inversely related to deer recruitment and population trends (Jones and Mason 1983). Management and research effort was subsequently directed at the role of predation in initiating the deer declines on northern Vancouver Island.

Wolf Numbers and Distribution

Historically, wolf numbers never appeared to be numerous on Vancouver Island. Bounty records indicated a peak of 140 wolves in 1909 (the first year of record), then quickly declined to less than 20 per year through the late twenties to 1955, when the bounty was terminated (Hebert et al. 1982). During the fifties and sixties, wolves were seldom observed on the Island. Concern over their welfare resulted in total protection from hunting and trapping, and by 1970 an "endangered species" designation was considered for Canis lupus crassodon (Hebert et al. 1982). Evidence of wolves began to increase in the early seventies, and by 1976 wolves were observed in all M.U.'s on Vancouver Island. Numbers increased to the extent that the hunting season was reinstated in 1977 and the trapping season in 1979.

From apparently very low numbers, the wolf population on the Island expanded to the point where, in less than a decade, they were considered abundant. Speculation as to the source for repopulation was centered on the emigration of mainland wolves, amalgamated perhaps by a natural increase in relic populations from the isolated northwest coast of the Island. A taxonomic study of wolves in British Columbia by Friis (1985) lent credence to these speculations. By comparing skull characteristics among pre- and post-1950 Vancouver Island and mainland wolf specimens, she concluded that the original Island population (C. l. crassodon), while not extirpated, is no longer distinct and cannot be reliably distinguished from coastal mainland wolves.

The difficulty of monitoring wolf population structure and change in coastal environments restricts the use of density estimates to intensive study areas. An easily acquired index to assess relative wolf abundance was developed based on reported sightings by deer hunters and search effort (number of wolves observed per hunter day x 100; Hebert et al. 1982). The hunter sighting index (HSI) provided the basis to monitor relative wolf abundance over time (Fig. 4) and to examine broad wolf-deer interactions.

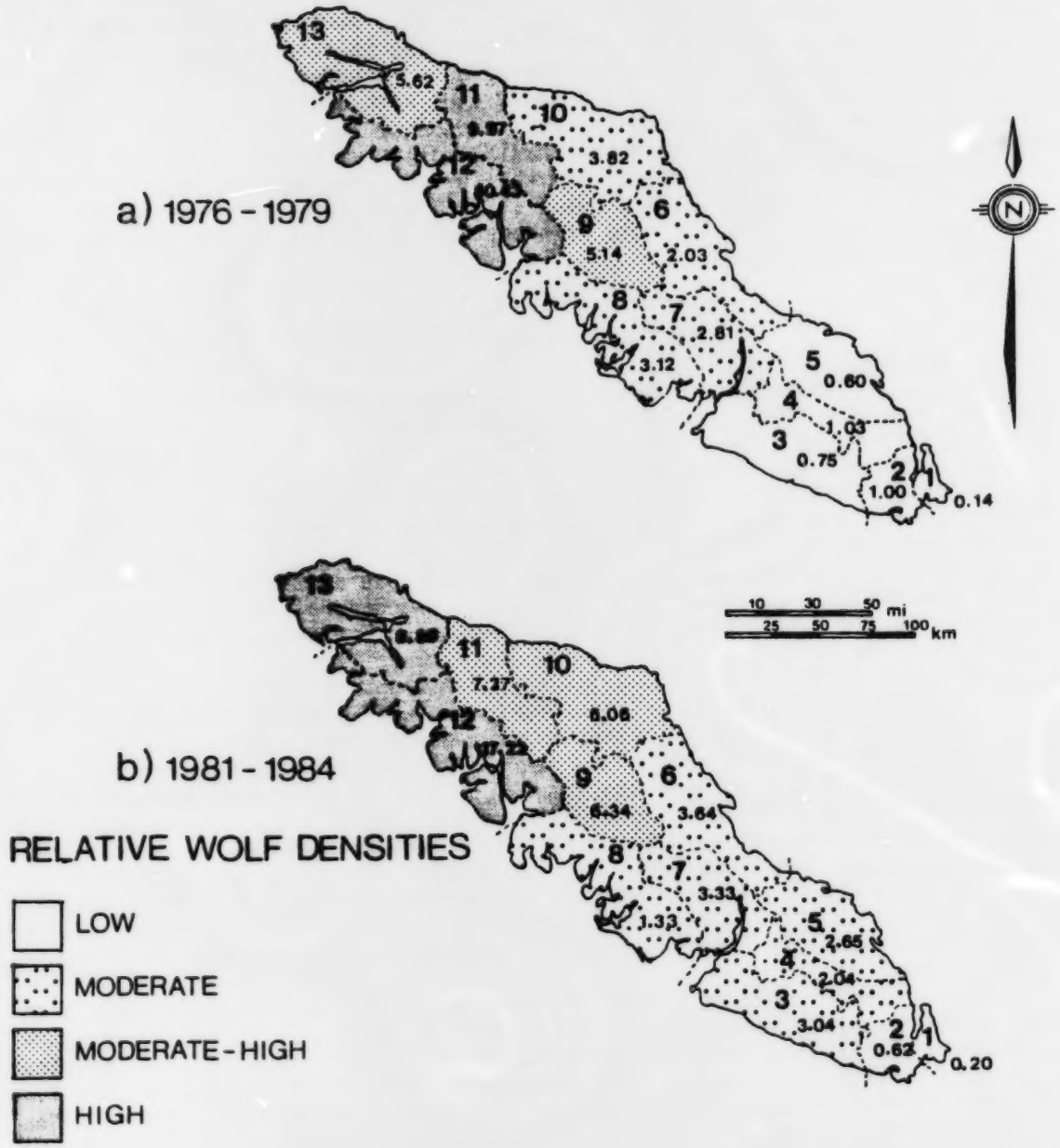

Figure 4. Relative wolf densities on Vancouver Island, 1976-79 and 1981-84. The hunter sighting index (HSI) is shown for each M.U. (from Janz and Hatter 1986).

Management Data

During the period of rapid deer declines on the north Island, the HSI indicated a general pattern of decreasing wolf densities from north to south Island (Fig. 4). Comparing deer population trends by wolf density class gave further insight into the relative effects of predation, hunting, and habitat factors. Deer habitat quality is considered to be poorer on the south Island than on the north Island due to advancing succession from early clearcut logging, resulting in large expanses of second-growth forest, as opposed to a more recent development pattern of early succession/old growth on the north Island (Hebert 1979). Despite habitat quality, deer populations on the south Island increased over the 1976-81 period, while populations were stable to declining in areas of moderate wolf densities, and rapidly declining in areas of high wolf densities (Fig. 5). Due to access and proximity to population centres, hunting pressure (both legal and illegal) is also generally higher on the south Island. This evidence further substantiated that the deer declines were not initiated by predisposing factors such as habitat quality, winter severity, or legal and illegal hunting.

Research Data

A study of food habits and social organization of wolves in the Adam River (M.U.1-10) was initiated by Scott (1979) in 1978, followed by Hatter (1984) who investigated the causes of low deer recruitment in the same study area from 1980 to 1982. Wolf densities within summer/fall home ranges were estimated at 1 wolf/6-15 km^2 (Scott 1979), with densities of 1 wolf/12-17 km^2 estimated for the watershed (Hebert et al. 1982). The two wolf packs studied by Scott (1979) maintained separate home ranges in 1978, and deer number trends were associated with degree of wolf activity, with largest declines occurring within the 90% home range and largest increases occurring in the buffer zone between pack home ranges (Hebert et al. 1982). By 1981, however, the buffer zone was eliminated by the expansion and overlapping of pack ranges in response to declining prey availability (Hatter 1984).

Food habits, documented in both studies, indicated that deer were the major prey item, accounting for 80% of the annual diet. Elk and beaver were secondary food sources. Over the summer period (June-August), fawns comprised 47 to 63% of the diet, with an estimated 5 fawns consumed per adult deer. Hatter (1984) documented a 63% mortality rate of radio-collared fawns by the end of August, with wolf predation accounting for two-thirds of the mortality. Accidents, disease, parasites, and malnutrition did not appear to be limiting recruitment. He concluded that wolf predation was the primary factor limiting deer recruitment. Bear and cougar predation and hunting harvest were likely additive mortality factors, but were not responsible for initiating deer declines.

Estimates of adult deer mortality rates were derived from a study investigating relationships between deer behaviour and second-growth forest management in the Nanaimo watershed (M.U.1-05) over the period 1982 to 1986

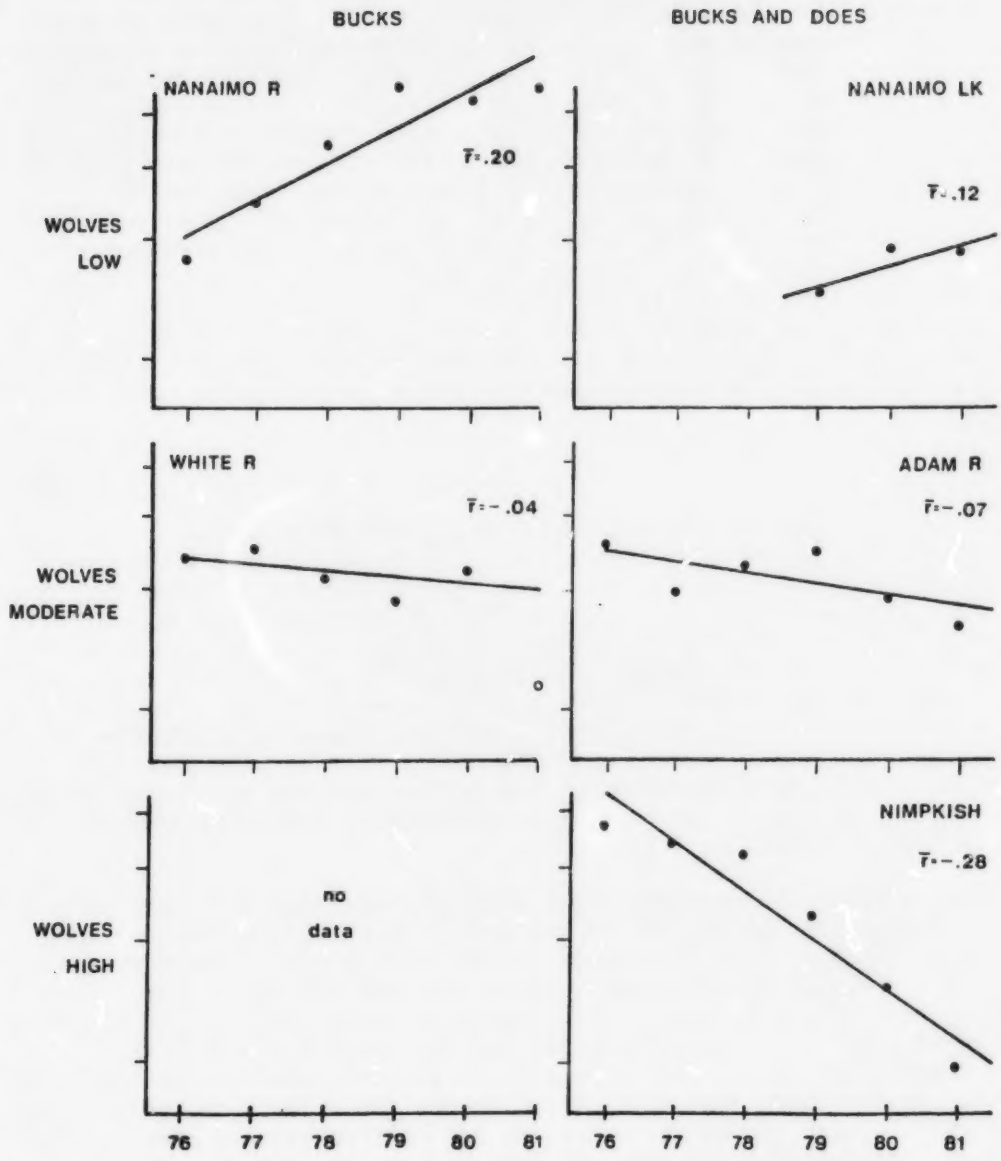

Figure 5. Rates of increase ($\bar{r}$) for deer herds in 3 wolf density regions on Vancouver Island. Regression lines were calculated from $\log_e$ deer/km index on year (from Hatter 1982).

(McNay and Doyle 1987). Prior to wolf removal, annual mortality rates of collared adult does was estimated at 23%, compared to a post-removal average of 4% per year by wolves. Cougar predation on collared deer was estimated at 1.3% per year throughout the study. The high mortality rates of adult deer by wolf predation corroborated the observed 25% annual declines in the population index for the Nimpkish over the 1978 to 1981 period.

Following on the management and research indications that wolf predation was the major factor limiting deer populations, an experimental wolf removal project was initiated in 1982 to further test the wolf predation hypothesis and to evaluate the effectiveness of trapping as a control technique. The study was designed to allow comparisons between a removal zone and a non-removal zone and between pre- and post-treatment periods within zones (Atkinson and Janz 1988). In addition to estimation of wolf densities based on telemetry and observation of wolves and wolf sign, scat transects were also used to monitor relative wolf abundance. Deer response was monitored by summer productivity counts (fawns/ 100 does), spring recruitment (% juveniles) and spotlight counts (deer/km). Over the 4 year study period, 64 wolves were killed in the removal zone (RZ), while 5 wolves were trapped and collared in the non-removal zone (NRZ). Estimated wolf densities in the RZ were reduced from an initial 1 wolf/23 to 25 km^2 to a low of 1 wolf/194 to 242 km^2 in the winter of 1984/85.

Following initiation of wolf control, RZ productivity was significantly higher than NRZ values over the study period (Fig. 6). In 1987, control was terminated in the RZ and initiated in the NRZ, resulting in significantly lower and higher counts, respectively. Similarly, juvenile recruitment in the RZ increased in response to reduced wolf numbers, while NRZ recruitment was lower but fluctuated over the study period (Fig. 7). The population index for both zones was significantly different between the pre- and post-removal periods (Fig. 8). The difference was more pronounced in the RZ, however, there was no significant difference between zones in the post-removal period.

Results from the RZ clearly illustrated the positive response of deer to reduced wolf densities. Trapping proved to be an effective, albeit labour-intensive control technique (mean annual wolf mortality rate in the RZ was 59%). Results from the NRZ were more ambiguous. This ambiguity was exemplified by comparing the 1984 August count of 23.2 fawns/100 does to the following spring recruitment value of 20.3%. The fawn count obviously underestimated true fawn production in the population. By the end of the project, it was learned that periodic removal of wolves by local residents throughout the study period was responsible for the data anomalies (Atkinson and Janz 1988). As the majority of this wolf removal likely occurred during the fall and winter (between summer productivity counts and spring counts), it appears that low fawn counts were indicative of both direct mortality and the influence of wolf presence on hiding behaviour. With reduced wolf numbers during the fall and winter, fawn survivorship was relatively high as reflected in the spring counts.

Although the experimental design was confounded, the data from both zones provided useful information on the relationships between estimated wolf

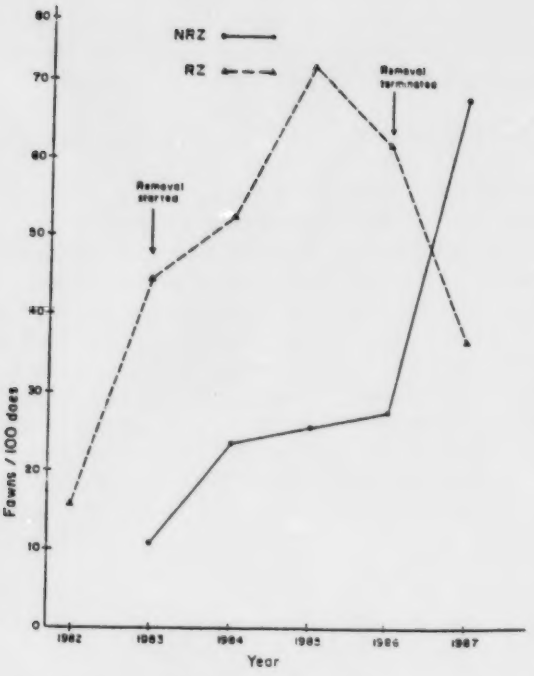

Figure 6. Fawns per 100 does in the removal zone (RZ) and non-removal zone (NRZ)(from Atkinson and Janz 1988).

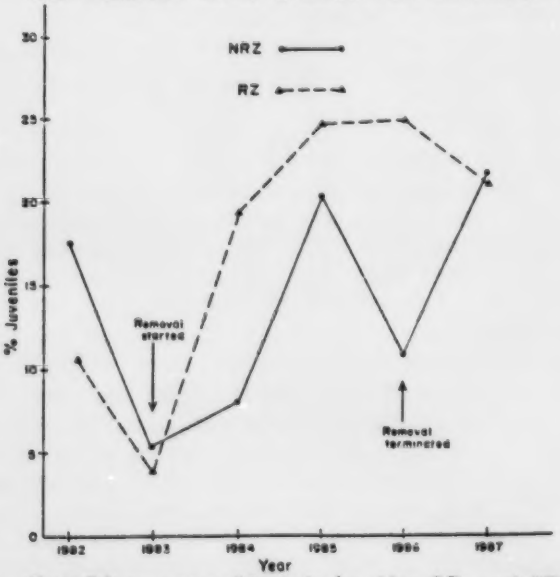

Figure 7. Yearling recruitment in the RZ and NRZ (from Atkinson and Janz 1988).

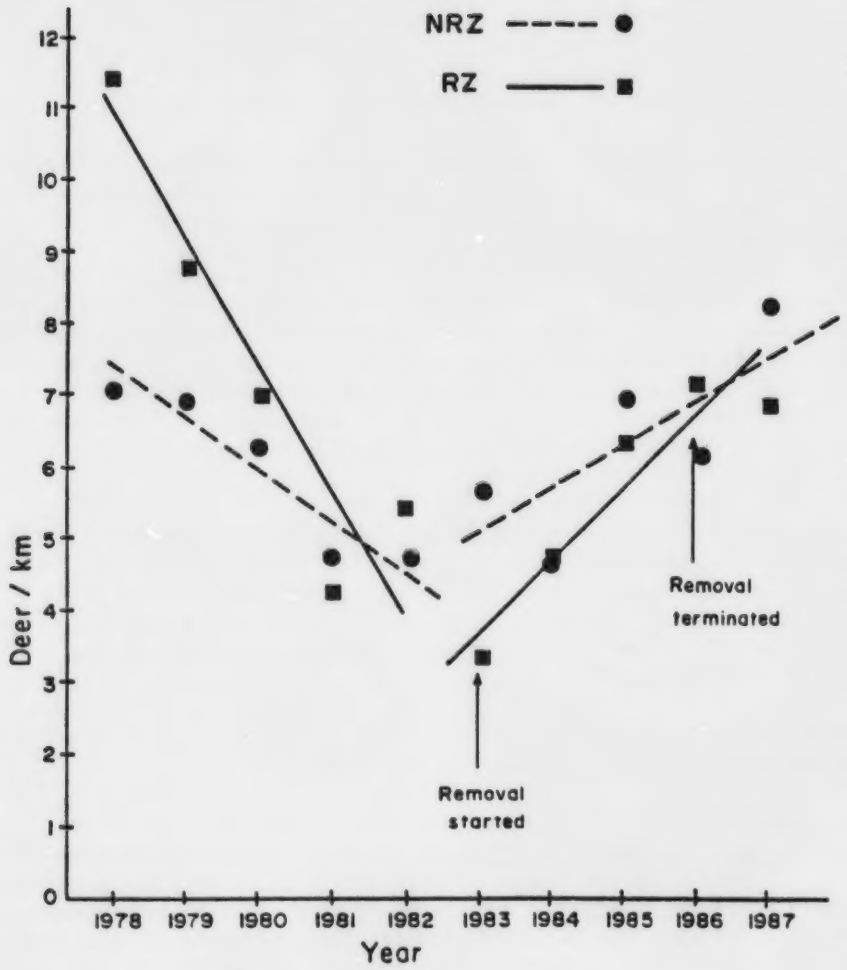

Figure 8. Pre-wolf removal and post-wolf removal deer population trends between the RZ and NRZ (from Atkinson and Janz 1988).

densities and deer population parameters. Fawns/100 does and spring recruitment in the RZ were significantly related to fall wolf densities (Atkinson and Janz 1988). Favourable survivorship of deer fawns at densities of 1 wolf/50 km^2 or greater was indicated (Fig. 9). Significant relationships between the winter scat index and recruitment, and the summer scat index and fawn:doe ratios, were also documented for both zones (Figs. 10 and 11). Relatively high values of fawn production and recruitment were evident when mean seasonal scat transect values were less than approximately 0.15 scats/km. Scat transects are being maintained in the study area and appear to offer an effective field technique for monitoring relative wolf abundance and evaluating effects of predation on deer population status. Continued data collection will further refine relationships among wolf densities, scat transects, and the HSI to aid the monitoring of wolf-deer interactions over large areas.

Management of the Predator/Prey/Habitat System

Wolves on Vancouver Island have caused substantial declines in deer numbers under diverse environmental conditions, with no indications that declines were initiated by predisposing factors of habitat degradation, winter severity, or overhunting. Factors such as the small size of black-tailed deer, availability of alternate food sources (including waste disposal sites), and possible influence of logging practices that may enhance the ability of wolves to predate on deer by reducing search time (concentration of prey in habitat patches, travel on logging roads), appear to contribute to the vulnerability of deer to wolf predation. In areas where wolf numbers have not been artificially reduced, there has been no natural recovery of deer numbers, and one can expect maintenance of a low equilibrium for several years (Nelson and Mech 1981; Gasaway et al. 1983).

The Nimpkish experimental wolf control project provided the basis for the development of a wolf management strategy for Vancouver Island. As a control technique, trapping was proven to be an effective method. Deer numbers responded positively to reduced wolf densities. In addition to the Nimpkish results, dramatic deer responses to wolf control were also documented in the White River (M.U.1-10), an area that has been subjected to wolf removal by a public trapper since 1982. The population index in 1982 had reached a low of 3.5 deer/km. In response to reduced wolf densities, mild winters, and good deer habitat, the population increased to almost 20 deer/km in 1988.

The research data also suggested that juvenile recruitment (spring classified counts) must be used in conjunction with summer fawn:doe ratios to monitor effects of predation on fawns. The latter measure can be confounded by the possible influence of predation pressure on deer hiding behaviour, while the former measure is a better indicator of actual survivorship of the fawn cohort accounting for all mortality factors. The removal of wolves by the public from the non-removal zone also has important management implications. Passive response by management agencies to wolf predation can lead to control initiatives by the local public, with all the inherent problems associated with such

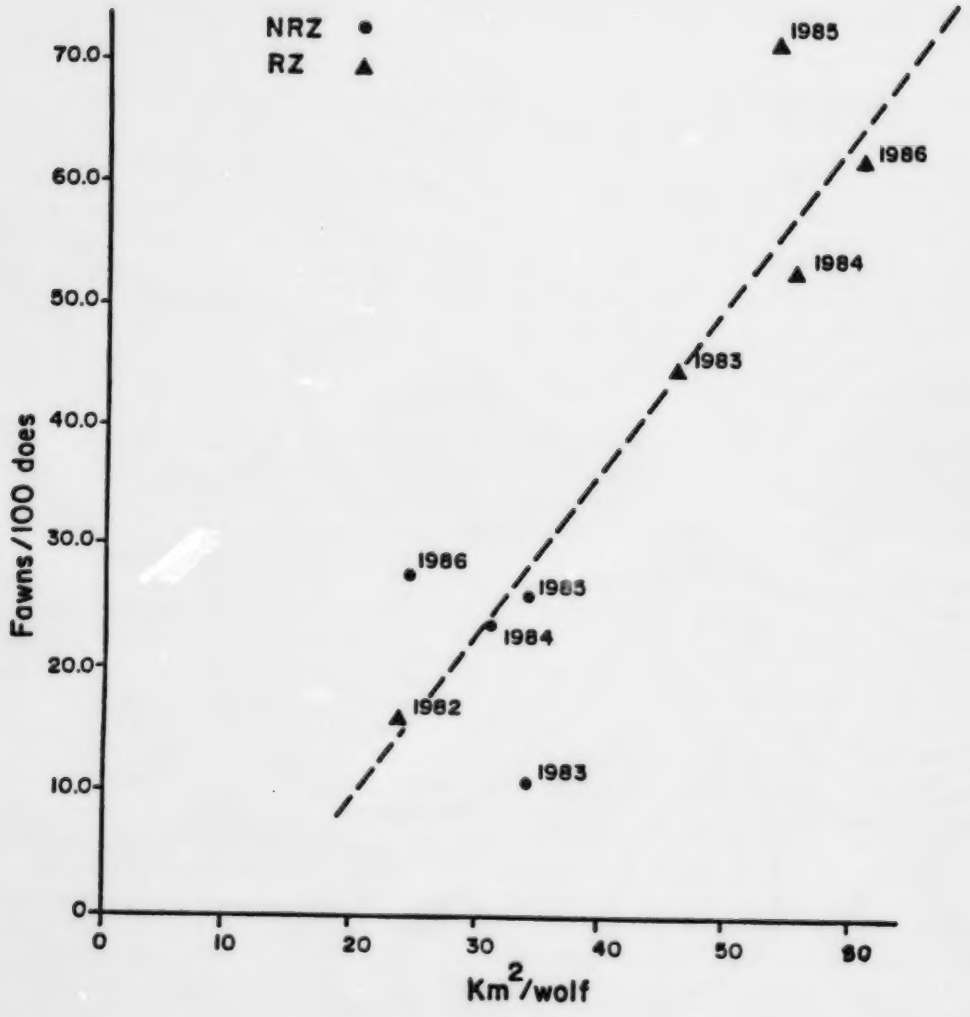

Figure 9. Relationship between fawns per 100 does and estimated wolf density in the removal and non-removal zones, 1982 to 1986 (from Atkinson and Janz 1988).

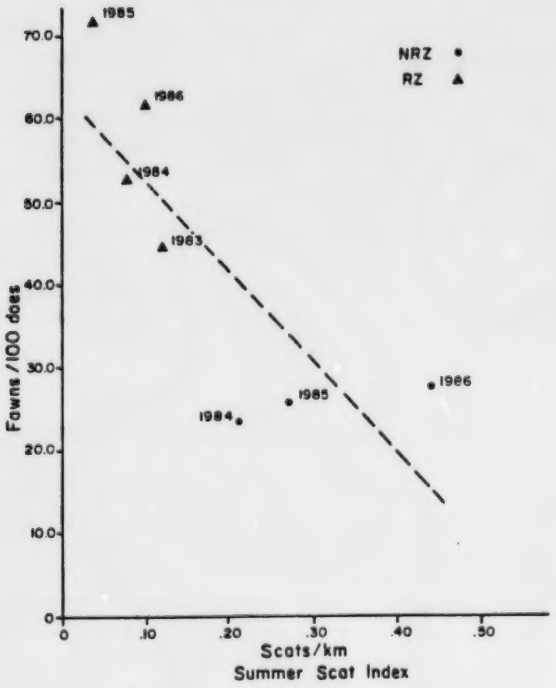

Figure 10. Relationship between fawns per 100 does and the summer scat index for the removal and non-removal zones (from Atkinson and Janz 1988).

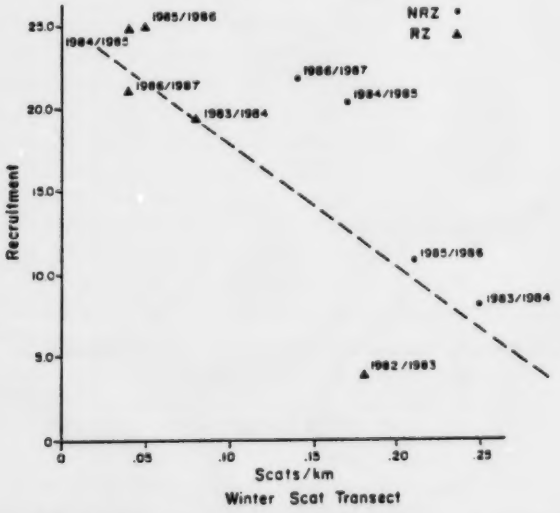

Figure 11. Relationship between juvenile recruitment and the winter scat index for the removal and non-removal zones (from Atkinson and Janz 1988).

activities, including the use of techniques that may be inhumane and/or ineffective in reducing wolf numbers.

An operational wolf control program was initiated on Vancouver Island in 1986. Objectives of the program were: to reduce wolf numbers to 1 wolf/100-150 km^2 to allow recovery of depressed deer herds; to initiate wolf reduction as required to minimize drastic deer declines and subsequent recovery time; and, to ensure the continued existence of wolves on Vancouver Island (Janz and Hatter 1986). The program was designed to encourage public trappers to trap wolves during the regular trapping season by providing traps on a loan basis and sponsoring training workshops. A few proficient trappers were also hired on contract.

Due to access restrictions and priorities for deer production, approximately 50 to 60% of the Island will not be subject to wolf control over the approved 3-year period of the present program. Approximately 150 wolves have been trapped during the first 2 years, and preliminary results (Janz 1988) indicate positive results where control was initiated prior to drastic declines in deer numbers. On the north Island, especially in M.U.'s 1-12 and 1-13, few wolves have been trapped and deer numbers remain at very low levels. The program will be fully evaluated in 1989. An important aspect for evaluation will be how effective regular hunting and trapping seasons will be at maintaining reduced wolf densities, and the possible need for periodic contract trapping and/or alternate control techniques to meet deer and wolf management objectives.

Discussions of predator-prey relationships and, more specifically, the perceived need for predator control often tend to focus only on the topic species, without adequate consideration of the characteristics of the entire system. Planning for the provision of high quality habitat is obviously the most important long-term management activity required to maintain all wildlife species. On Vancouver Island, logging and forestry practices are the major forces manipulating wildlife habitat, and as such, dictates that an integrated management approach is required to supply the habitat requisites of wildlife. To ensure deer numbers sufficient to meet management objectives, approximately 40,000 ha of old-growth timber winter ranges have been deferred from logging on Vancouver Island and the adjacent mainland. Value of this timber to the forest industry is substantial (B.C. Ministries of Environment and Forests 1983). In addition to the values of old growth, research and management programs aimed at investigating interactions between wildlife habitat and second-growth forests and the use of various silvicultural techniques to enhance deer and elk habitats have received significant effort since 1981 (Eastman and Ellis 1981). When deer numbers are being controlled at levels far below existing habitat carrying capacity by wolf predation, attempts to invest in activities designed to maintain and increase deer habitat are difficult to implement. Relatively high deer densities are required to help justify retention of old growth and enhancement of second growth for wildlife habitat, especially under current economic and political climates.

Another important characteristic of the predator-prey complex on Vancouver Island that is often overlooked is that it is a multi-predator system.

Deer are the major prey item of cougar (Dewar and Dewar 1975) and, although a minor component, contribute seasonally to the black bear's diet (Hatter 1984). The interactions between wolves and cougar and implications of reduced deer numbers on the status of cougar on Vancouver Island have not been investigated, but it can be speculated that declines in cougar numbers over the past decade, as indicated by the cougar HSI, is due to lower prey availability. Abundant deer numbers are thus required to maintain long-term viable populations of both wolves and cougar on Vancouver Island.

The deer population is also a valuable resource with respect to human benefits associated with hunting and non-hunting recreational activities. Deer harvests from Vancouver Island typically account for 25% to 40% of the provincial deer kill, and a significant portion of people involved with direct non-hunting activities focus on deer and elk. Ungulates were second to marine mammals as the species group generating "most interest" in a recent survey on non-hunting activities (Reid et al. 1986). The recreational and economic benefits associated with these activities are significant, and public demand can be expected to remain strong for the provision of recreational opportunities associated with deer and elk.

Black-tailed deer can thus be considered to be the major component of the predator-prey-habitat system on Vancouver Island. Low deer populations over long time periods can be expected to result in very low numbers of wolf and cougar, low levels of human participation in recreational activities associated with these species, and a further reluctance to implement habitat prescriptions. Characteristics of the system dictate that options must exist to manage all factors affecting deer populations on Vancouver Island. Experience also indicates that managing the system to prevent major deer declines is much more effective and feasible than attempting to aid recovery from low numbers.

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IMPACTS OF WOLF PREDATION ON ISLE ROYALE MOOSE POPULATIONS

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SUMMARY

After 30 years, the studies of moose and wolves on Isle Royale continue to surprise. The stable wolf numbers of the 1960's led to a gradual increase of the moose population to a high of 1200-1700 by 1970. As the moose population declined the wolf numbers increased, and predation rates (especially on calves) escalated dramatically. With no recruitment, the moose population became increasingly old, suffered high rates of arthritis and malnutrition, and offered relatively vulnerable prey to the wolves. Only after a dramatic decline of the wolves from 50 in 5 packs in 1980 to 14 in 3 small packs in 1982, did the moose population recover. The number of calves in the population in 1982 was the highest ever recorded, indicating that the decline throughout the '70's was due to predation and not a lack of food.

INTRODUCTION

Since Durward Allen and David Mech initiated the wolf study program in 1958, Isle Royale has been the focus of worldwide interest in wolf-prey dynamics (Mech 1966). After 30 years, the results from Isle Royale continue to play a pivotal role in the scientific understanding of predator-prey and ecosystem dynamics. We are continuing to find that the island can only be characterized by a complex and sometimes subtle interplay of the many factors that constitute an island ecosystem.

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Our objective in this research has been to clarify the nature of predator-prey interaction between naturally-regulated populations of wolves and moose, with emphasis on mechanisms of population regulation for these two species. We have only recently been able to address the other levels of the ecosystem, meaning the moose food supply and the factors affecting its consumption and replenishment (Risenhoover 1987, Bradner 1975). In the next decade, you will see the emergence of ecosystem level understanding from the Isle Royale research studies, including the impacts of acid rain and the deposition of contaminants.

Based on an assessment of moose calf recruitment and wolf predation rates during 1959-61, Mech (1966) argued that wolf predation was maintaining a stable moose population below limits imposed by moose food supply. Subsequent periods of investigation concentrated on assessment of moose population trends and population dynamics of other Isle Royale mammals. Census techniques used throughout the 1960's did not allow accurate determination of moose population size, but by the late 1960's it was clear that it had perhaps doubled, with at least 1200 moose present. A series of severe winters beginning in 1969 accentuated the depleted food supply for moose, and set the stage for a major moose decline. During the early 1970's moose declined by 50%, while a previously stable wolf population began a sustained increase. Updating Mech's conclusions, Peterson (1977) felt that wolf predation controlled moose density, but only within limits dictated by food supply. He interpreted the moose decline of the early 1970's as a shift to a lower density equilibrium attributable to forest maturation, especially in the 1936 burn. From this conclusion followed the prediction that moose should remain at a lower density.

Moose were clearly held at a low level during the late 1970's by a record-high wolf population (Peterson and Page 1983). The increase of moose that followed the wolf crash of 1980-82 disproved the hypothesis of Peterson (1977) that wolf predation sensitively adjusts moose population levels to food supply (i.e. without lags). Peterson *et al.*(1984) recently published a new hypothesis based on the idea that Isle Royale wolves and moose will continue to follow a long-term cycle with a period length of about 30 years. This cyclicity is predicted to be common to high density wolf-prey systems. It has only been positively documented for Isle Royale but northern B.C. caribou (Bergerud and Elliot 1987) and arctic caribou populations (Haber 1977) show cyclic tendencies.

STUDY AREA

Isle Royale National Park is composed of 1 large island measuring 544 km^2 plus numerous off-shore islands with very little area, located about 20 km from the north shore of Lake Superior (Figure 1). The island has formed as the uptilted edge of numerous layers of metamorphosed bedrock of igneous and sedimentary origin, resulting in a long and narrow island with a high ratio of shoreline to area. Boreal forest vegetation dominates the island with white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) occurring in greatest abundance. At higher elevations on the southwest end of Isle Royale is a hardwood forest dominated by sugar maple (*Acer sacharrum*) and yellow birch (*Betula allegheniensis).* Glacial till is sparse and soils are thin and poorly developed on the northeastern 2/3 of the island, while on the southwestern 1/3, glacial till is thick and soils are more developed. North-facing slopes are steep, while south-facing slopes are quite gradual. Each winter, all interior lakes and protected harbors on the island's periphery are frozen from November or December until April. Extensive shelf ice commonly forms along most of the island's shoreline, and every 2-3 years a rough ice bridge to Canada forms briefly in mid-winter. Since 1971, exceptionally smooth ice bridges formed only during 1976-77 and 1978-79.

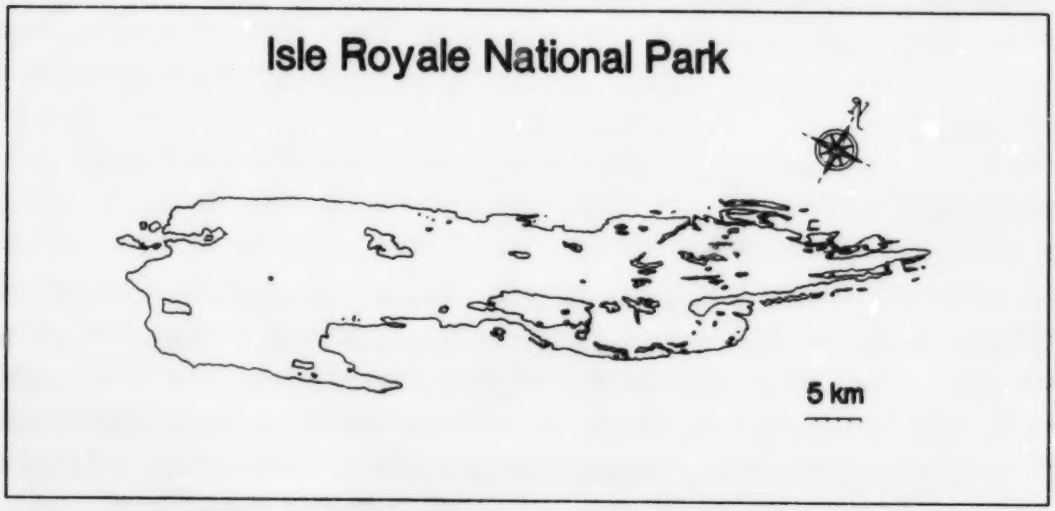

Figure 1. Isle Royale National Park is 544 km^2.

The island is usually snow-covered from December through March. During mid-January to early March snow depths in open areas are usually about 50-60 cm, with extreme depths occasionally reaching 100 cm.

About 2/3 of the mammalian species present on the adjacent mainland have never colonized Isle Royale. Only moose and beaver are prey for the Isle Royale wolves. In winter, wolves are almost entirely dependent upon moose, with beaver available only occasionally during midwinter thaws.
In order to ensure a complete sanctuary for the wolf population, Isle Royale National Park is closed to visitors from November to mid-April. The only human inhabitants during the closed season are members of the research and monitoring crew, who gather data primarily from aircraft. During the summer visitor season, most human activity is restricted to hiking trails, with closures instituted in areas with a history of intensive wolf use (dens and summer homesites).

Research into natural population regulating mechanisms for wolves is hampered by continuing persecution by man. Isle Royale National Park provides the only site in the world where intensive studies of wolves have been carried out in the absence of important human influences. The prey population fluctuations of the past decades provide important insights into natural wolf population responses to changing food supply.

METHODS

Wolves

Almost all wolf observations were made from aircraft during an annual winter study beginning about 20 January and extending for 7 weeks. National Park Service policies have not allowed handling of any wolves, precluding use of radio-telemetry to locate wolves for observation. Wolves were located by snow-tracking from light aircraft (Aeronca Champ, Citabria or Piper Supercub) on a daily basis if weather and snow conditions permitted. Wolves have become accustomed to the presence of the aircraft and exhibited virtually no avoidance behavior. Wolves were observed with 7X wide-field binoculars and, since 1984, with a gyroscope-stabilized monocular viewing device. Wolves were back-tracked whenever possible to their previous

location, ideally providing complete coverage of travels and kills made since last observed.

Wolf packs were distinguished by size, location, and identifiable pack members (usually alpha, or dominant individuals). Packs were generally cohesive, and frequent observations allowed us to identify packs easily. Individual wolves were often recognized on a day-to-day basis by body conformation, pelage appearance, and, especially, tail characteristics. In rare cases, individuals were sufficiently unique that year-to-year recognition was possible. Social status of individual wolves was inferred from behavioral interactions among pack members (Peterson 1977).

Aside from major packs, single wolves and small, non-territorial packs numbering up to 5 wolves were tracked and observed opportunistically. A complete count of the wolf population was made at least twice during each annual study, more commonly several times.

During summer, ground personnel gathered data on wolf food habits and reproduction. Traditional dens and homesites were checked each year, and, if occupied, spontaneous and induced howling provided some data on the number of pups present. Abandoned sites were thoroughly examined for prey remains and scats, and additional scats were examined throughout the island during approximately 800 km traveled annually.

As in previous studies of Isle Royale wolves and moose , light aircraft were used to observe interactions of wolves and moose in midwinter, from approximately mid-January to early March. A total count of wolves was made each winter after the pattern established by Mech (1966). During daily flights, weather permitting, wolf packs and individuals were located by snow-tracking, and we tried to maintain, through back-tracking, a complete travel and predation record for the major packs on the islands. In some cases a complete kill record could be reconstructed in the absence of a complete travel record; complete travels were available for 66% of the time during which kills were recorded.

Virtually all kills were examined on the ground during winter or the following summer in order to gather data on age, sex, and condition of the victim. Since utilization of carcasses was highly variable and depended on the elapsed time

between the kill and the examination, we estimated food availability based on assumed edible prey weights provided by Peterson (1977). Additional moose carcass remains were located opportunistically, especially during the intensive summer ground searches of the island. Age was assigned to moose less than 18 months old on the basis of tooth eruption. For older moose we estimated age in years from growth annuli in ground molars or sectioned incisors (Sargeant & Pimlott 1959).

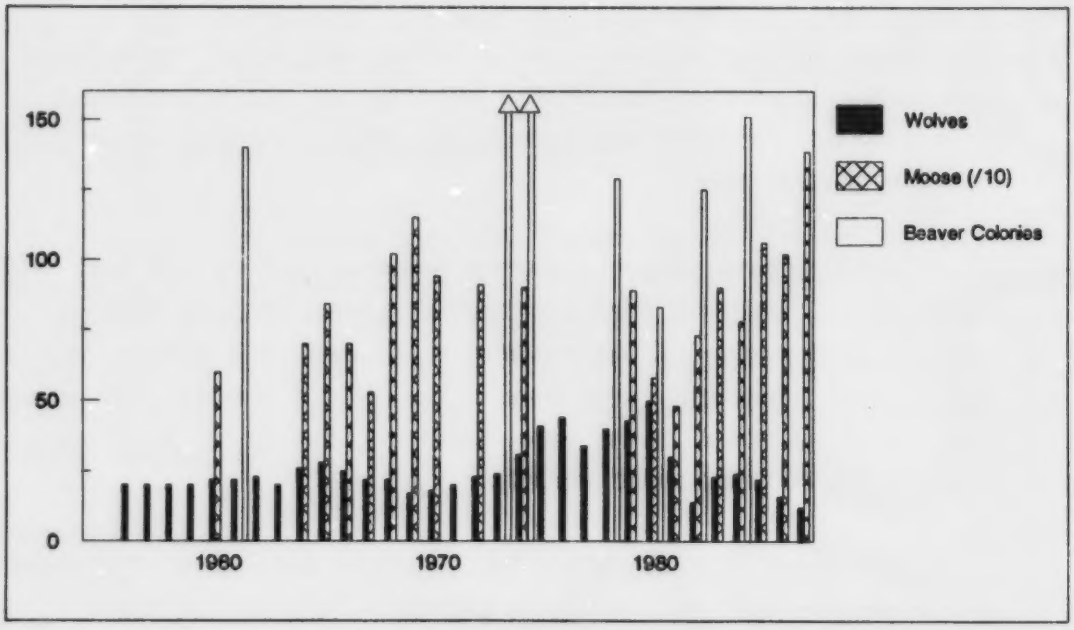

Figure 2. Population estimates from 1955 to 1987.

Prey

Moose and beaver were censused periodically throughout the study. A complete count of beaver colonies was made from aircraft in 1974, 1978, 1980, and 1982 by the same pilot and observer (Shelton and Peterson 1983). During 1969-83 moose population estimates were based on aerial sampling using stratified random

quadrats (Peterson 1977), a winter aerial index (moose/hr) and a summer ground index (moose/100 km). Summer and winter indices were significantly correlated (r^2 = 0.52, P<0.001). The quadrat counts in 1970, 1980 and 1981 were used as alignment points for the summer index. The estimates based on the summer index, the longest data set, were used to convert the winter index to an additional estimate of moose density. This annual best estimate, used in publications from 1980-87, was the average of all available estimates for a given year. A weighted estimate favoring aerial surveys is being developed. In this paper, the aerial survey estimates alone are used.

PREY POPULATION STATUS

The major prey species supporting Isle Royale wolves are moose and beaver. Throughout the 1970's both prey species declined and finally increased rapidly from 1980 to 1982 (Figure 2).

Beaver

Beaver increased to peak levels by the early 1970's, with the highest colony count obtained in 1974 (Shelton and Peterson 1983). Subsequent surveys in 1978 and 1980 revealed a steady decline to a low which corresponded to peak wolf numbers. Following the wolf crash of 1980-82 beaver numbers recovered, increasing from a mere 29% of the 1974 peak in 1980 to 53% of the peak in 1984.

The inverse correlation between wolf and beaver numbers suggests a strong influence exerted by wolf predation on beaver density. Equilibrium beaver density, defined by long-term average numbers, still appears to be responsive to forage abundance. For example, beaver colony density in Voyageurs National Park in Minnesota is 3 times higher than Isle Royale (Peterson, unpubl. data). Voyageurs National Park supports young successional stage forests with abundant aspen stands while Isle Royale forests are old with a high proportion of conifers. Wolf numbers and total land area are comparable in the 2 areas.

Moose

During the early 1970's moose numbers declined from the peak aerial estimate of at least 1,150. Jordan and Wolfe (1980) estimated that peak population size was 1,200-1,500, and we are now tending towards the highest estimate. A low point of about 500 moose was reached by 1977, and moose remained relatively stable at this low level until 1981.

The large cohort of 1981 signaled the beginning of recovery for the moose population. Calf abundance in October averaged 23 calves/100 cows during the decline from 1972-80. In October 1981, after the wolf crash, calf abundance stood at an unprecedented 61 calves/100 cows. During 1982/84 this dropped to 30-35 calves/100 cows, sufficient to provide an annual growth rate of about 5% for the moose population almost identical to the 6% rate of the late '60's. The moose population remained around 1000 from 1982-86.

We have hypothesized that wolves and moose at Isle Royale are fluctuating on a long-term cycle lasting about 30 years (Peterson *et al.* 1984). As the single most important mortality factor operating on this moose population, wolf predation has obviously been responsible for the major trends in moose numbers.

WOLF POPULATION CHANGES

In the early 1970's, the wolf population reached a maximum of 31 animals in 1974 in only 2 packs (Peterson 1977). From 1975-80 the wolf population increased each year except 1977 and fluctuated between 34 and 50 individuals (Figure 3). Additional packs became established during this period, until 5 were present in 1980. New packs appearing during this period were Middle Pack (1975), Southwest Pack (1976), and Harvey Lake Pack (1980). In 1979 the West Pack, recognized since 1968, finally disappeared.

A wolf "crash" occurred from 1980-82, when the population plummeted from 50 to 14 wolves. One major pack, probably the Southwest Pack, disappeared completely, and all packs were greatly reduced. The only pack that we could trace with certainty from 1980 to 1981 was the Harvey Lake Pack. Both the West Pack II and the East Pack II used portions of the island similar to previously recognized

packs, but the drastic changes in pack size and the lack of recognizable wolves precluded a determination of their origin. Similarity of pack boundaries between the two eras of wolf packs is likely due to the effects of natural features on pack territories and doesn't reflect a continuity of individual wolves.

Wolf numbers recovered after the crash of 1982, and the moose population stabilized by 1986 at about 1000. Since then a mysterious decline in the wolf population has occurred despite abundant food supplies. Concurrent with the wolf decline, moose have begun a remarkable increase to at least 1600 in 1988. Blood samples collected from wolves in the summer of 1988 have implicated a disease, parvovirus, as the most likely cause of the wolf decline. Further work is necessary to draw definitive conclusions, but current population numbers are clearly anomalous.

WOLF FOOD HABITS

From 1973 through 1980, wolf scat analyses showed beaver and moose to occur with roughly equal frequency in summer. During this time, an average of 82% of the summer moose occurrence was provided by calves. However, percent occurrence accurately reflects neither relative number of prey taken nor prey biomass (Floyd *et al.* 1978). Isle Royale wolves rely more heavily on beaver than other wolf populations feeding predominantly on moose, though moose still provide over 80% of summer food for Isle Royale wolves. Although adult hair in scats is uncommon compared to that of calves, adult moose provide the same prey biomass as moose calves. Based on relative numbers of prey, wolves kill more beaver in summer than any other prey and about 6 moose calves for every adult killed. When data from all 2,648 scats examined between 1975 and 1983 are grouped and compared to samples examined in 1958-61 and 1973, there is remarkably little change, except in the proportion contributed by beaver.

Beaver proportion increased from insignificance in the late 1950's to a prominent prey item when the beaver population peaked in the first half of the 1970's. It has since declined as the beaver population itself dropped. Previous conclusions that beaver constituted half of the wolf diet in summer were based solely on percent occurrence data. When these are converted to relative biomass it is clear that Isle Royale wolves continue to rely on moose in the summer as well as winter. Beaver muscle tissue has a higher caloric value than moose and beaver are the prey

most frequently taken by the wolves in summer. Moose, beaver, and snowshoe hare composed the following proportion of all prey occurrences: Kenai Peninsula (94%); Nelchina Basin (81%); Alberta (92%); Isle Royale, 1958-61 (88%); Isle Royale, 1973 (100%); Isle Royale, 1975-83 (90%).

In 1981-83 wolves apparently switched to a diet of primarily moose in summer. This accompanied a dramatic rise in calf numbers on both an absolute and proportional scale. Significantly, beaver density increased between 1980 and 1982 after a significant decline since 1974. It seems that beaver could not increase without the wolf decline.

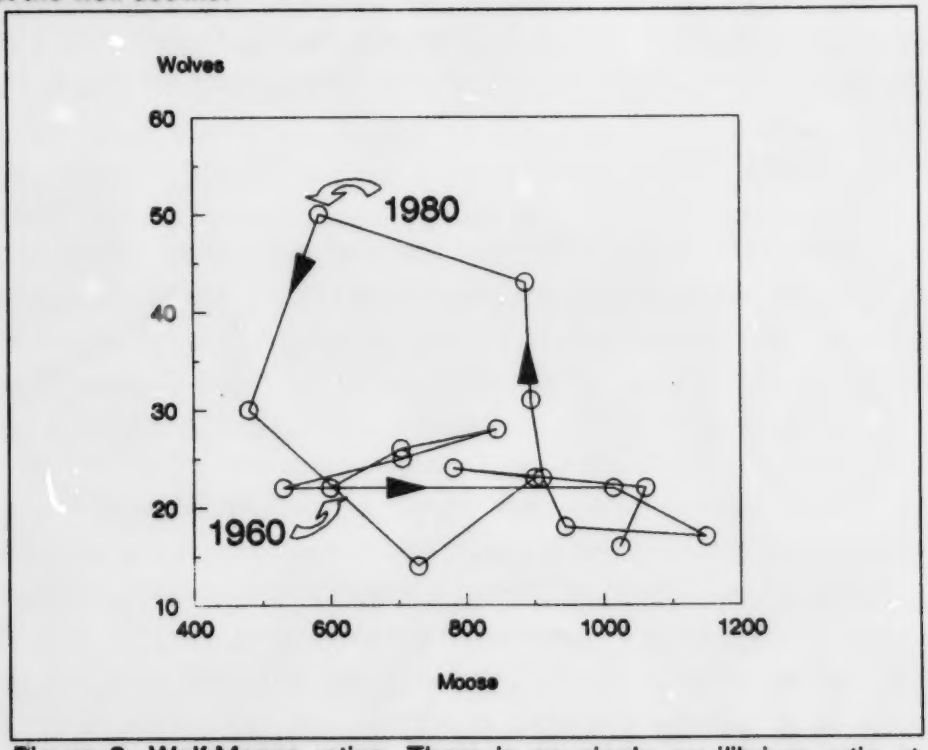

Figure 3. Wolf:Moose ratios. There is no single equilibrium ratio at these densities.

MOOSE AGE STRUCTURE

It is now evident that wolves and moose on Isle Royale interact in ways that cannot be simply described by linear models. The major confounding influence is the presence of long-term lags and cumulative effects in weather (Mech *et al.* 1987), wolf pack regulation and moose age structure. Wolf packs and wolf numbers are

only loosely related to moose numbers (Figure 3). Wolf predation caused continued decline of the moose population for almost a decade and the moose population was unable to escape predation effects until the wolves declined.

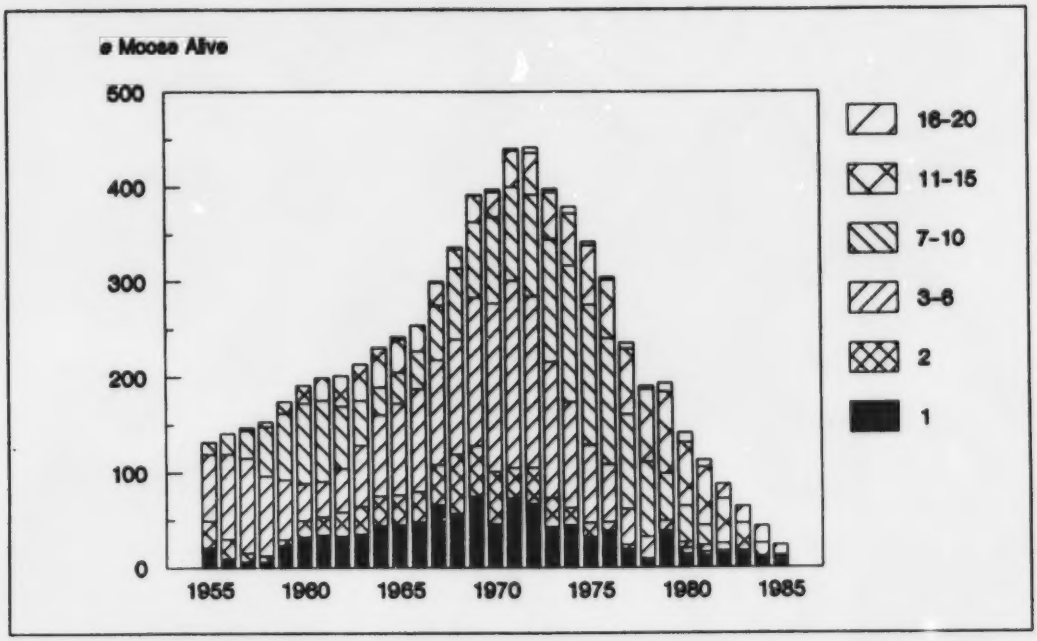

Figure 4. Moose age structure reconstructed from all moose found dead and accurately aged.

The 1800 moose collected over 30 years resulted in 1003 animals for which accurate times of birth and death could be determined. This allowed us to reconstruct the populations alive, with low precision from 1948 to 1953, moderate precision from 1954 to 1958 and high precision from 1959 to 1980. Relatively few of the moose alive in 1980 and born since have died to allow us to reconstruct recent populations (Figure 4). The population estimates derived from the reconstructed ages correlates well with the aerial survey estimates if it is assumed that about 1 moose in 3 that was ever born was recovered (Figure 5). The 1967 survey estimate is unrealistically low, and the 1979 estimate is too high. Since 1981, the reconstruction is clearly inadequate.

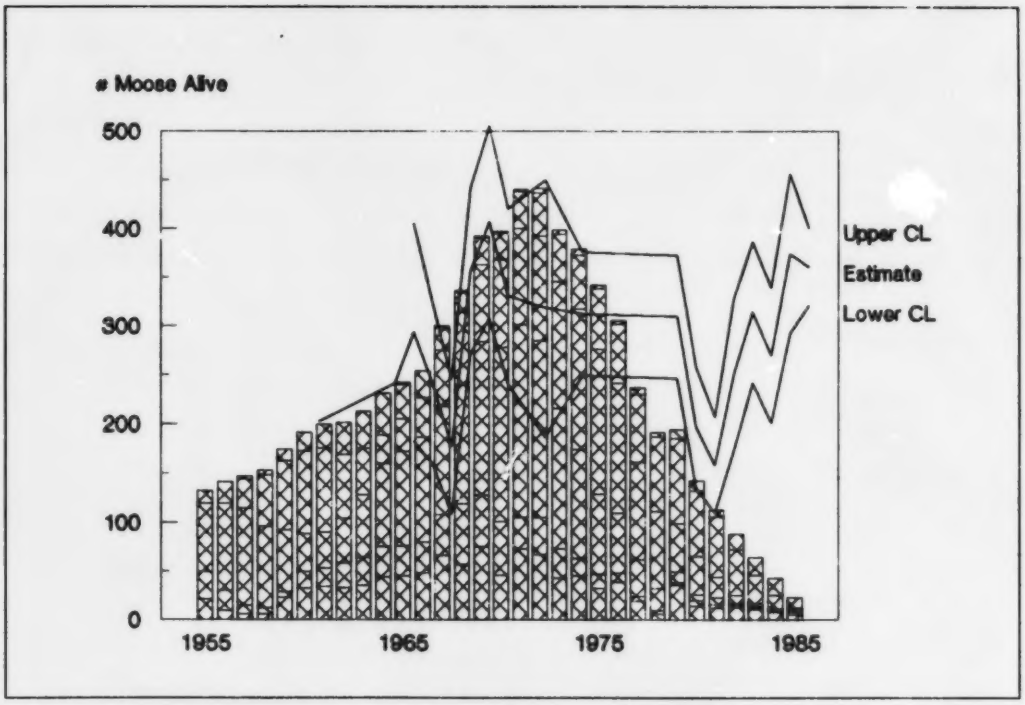

Figure 5. Comparison of population size from reconstructed age structure and aerial survey estimates. Survey estimates are divided by 3.

The drop in the number of calves from 1972 is greater than the decline in the total population, reinforcing again the critical importance of adequate recruitment of calves to sustain a population. Almost no calves survived the winter of 1978. From the aerial survey estimates, it appears that more calves were present in 1982, than the previous 4 years combined.

Also intriguing is the apparent lack of recruitment in the mid-1950's (Figure 6). The failure of calves to survive in the 1970's was due to the scramble competition of the wolf packs for the inadequate food supply and a resultant excessive rate of predation. It appears that similar competition occurred when the wolves were first attempting to establish territories on Isle Royale.

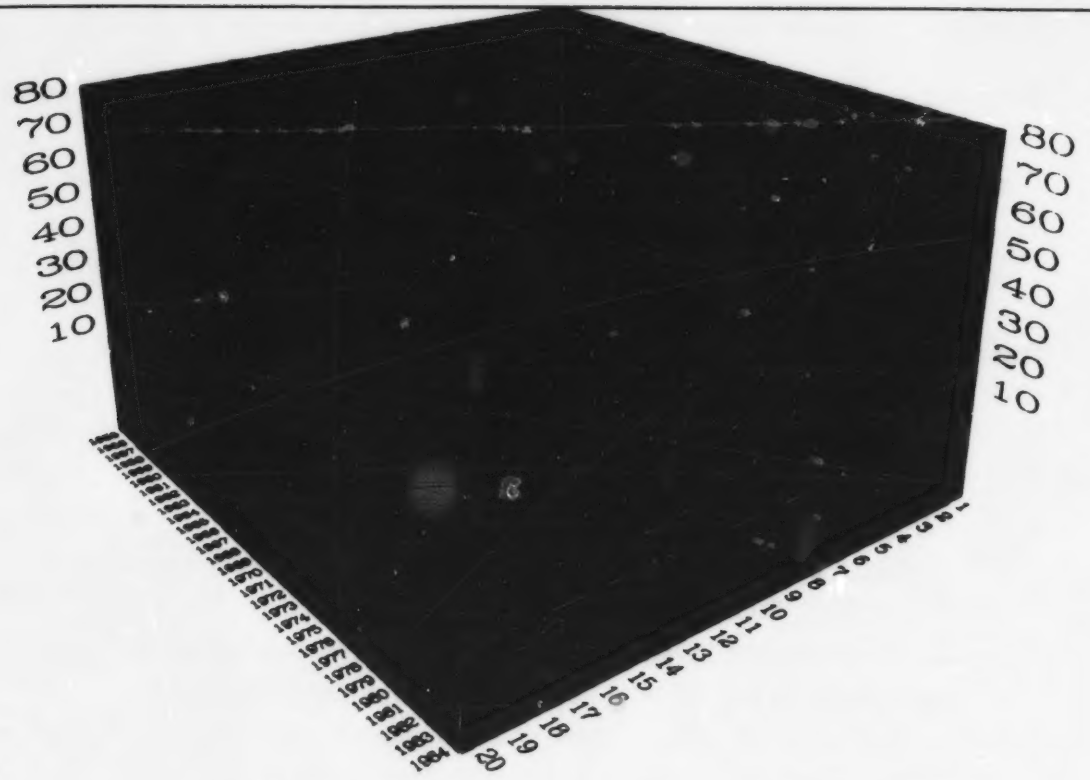

Figure 6. 3-D view of reconstructed moose ages showing lack of recruitment from the mid-1950's and the mid-1970's cohorts.

The discovery of the first low point in the 1950's and thus the first confirmatory evidence of cyclicity, was only possible because of the continuous and long-term nature of the Isle Royale dataset. Another 10 years will be needed to fully reconstruct the populations of the early 1980's and confirm or refute our predictions. Perhaps we can only afford a few such intensive and lengthy studies, but the risk of having none and being confined to short-term scientific understanding of our world is incalculable.

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CARIBOU-MOOSE-WOLF INTERACTIONS IN CENTRAL BRITISH COLUMBIA

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Woodland caribou (Rangifer tarandus caribou) populations in British Columbia have experienced major declines during the 1900's (Bergerud 1978). Caribou have disappeared from many areas of their historic range in southern and central B.C. (Stevenson and Hatler 1985). Those declines have often been attributed to overhunting and to habitat loss due to fires and logging (Edwards 1954, Bloomfield 1980). However, Bergerud (1974) concluded that the caribou declines were at least in part due to increased predation by wolves (Canis lupus). Bergerud and Elliot (1986) suggested that the colonization of British Columbia by moose (Alces alces) during the 1900's has sustained increased wolf populations and led to a higher predation rate and population declines in caribou.

The purpose of this paper is to evaluate the hypotheses:

1. Wolf predation is a major limiting factor of caribou populations in central British Columbia.

2. The wolf populations are sustained primarily by moose.

STUDY AREA

The study area included the Quesnel Lake area and Wells Gray Provincial Park (Fig. 1). The topography ranged from gentle mountains and plateaus in the Quesnel and Shuswap Highlands to steep, rugged peaks in the Cariboo Mountains (Fig. 1). The Interior-Cedar-Hemlock (ICH) biogeoclimatic zone occurs at low elevations up to about 1200-1350 m. (Lea 1986). The Engelmann-Spruce-Subalpine-Fir (ESSF) zone occurs above the ICH up to about 1800-2000 m.. The upper part of this zone consists of an open parkland forest type designated the ESSFmp. Alpine Tundra (AT) occurs above the ESSF zone. Snow accumulations in winter are very deep, usually exceeding 200 cm. in the mountains (B.C. Ministry of Environment 1985).

METHODS

The Quesnel Lake study started in 1984 and the Wells Gray Park study started in 1986. Each year,16 to 43 radio-collared adult, female caribou were monitored. In addition, seven moose

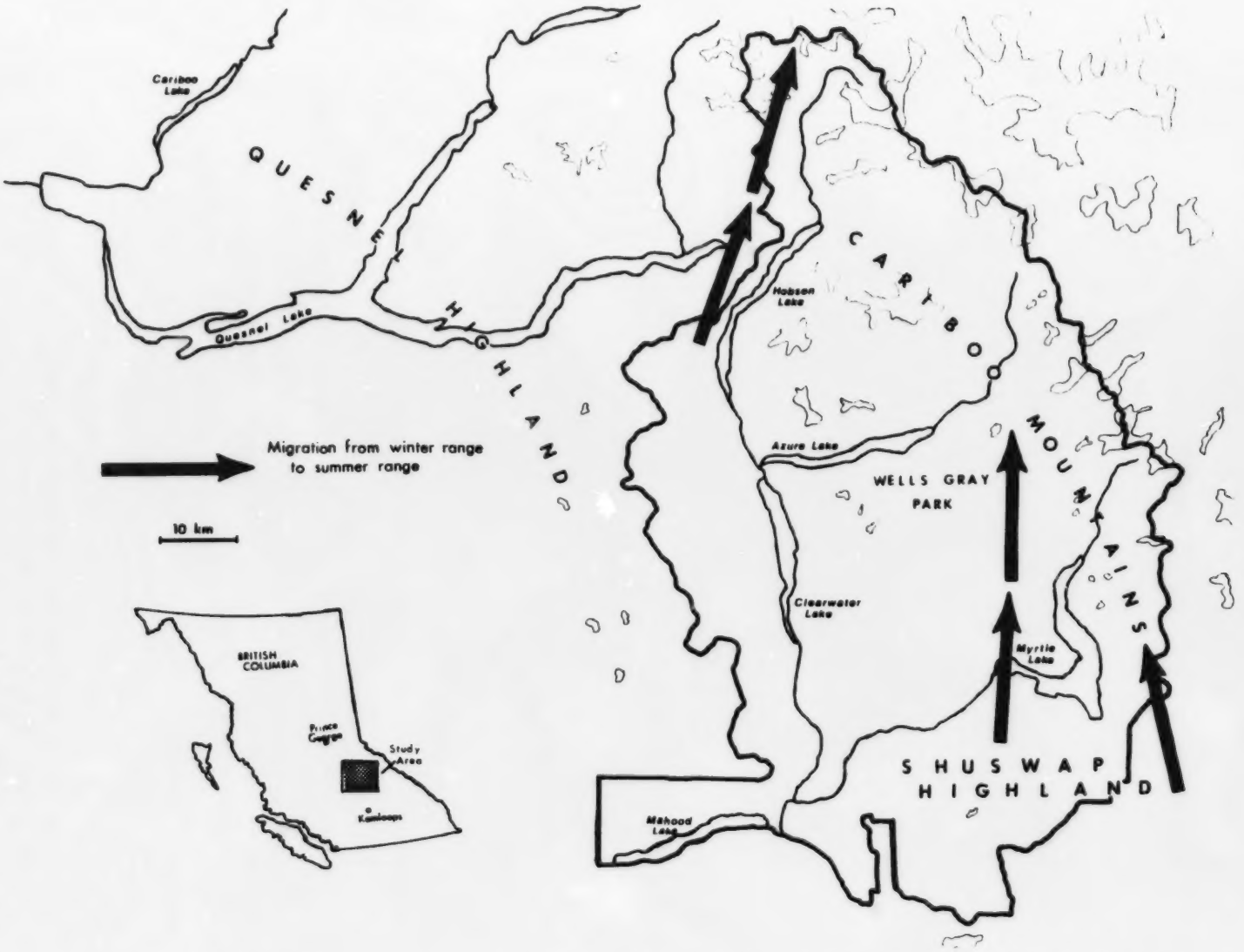

Figure 1. Map of study area and caribou migration patterns. Topgraphic regions and the 2250 m contour interval are shown.

and seven wolves were radio-collared and monitored. The radio-collared animals were located by telemetry from an airplane 2-4 times each month. Location, elevation and habitat type were recorded for each animal.

The radio-collars had motion-sensitive mortality sensors to indicate when animals had died. Dead animals were necropsied to determine the cause of death. Calf counts were conducted from a helicopter in June, August and October each year to determine the number of radio-collared caribou with surviving calves. A helicopter survey of the entire study area was conducted each March to count the caribou and to determine the proportion of calves in the population.

Wolf scats were collected throughout the year and analysed to determine food habits. The percentage occurance of prey hair in the scats was corrected based on the body size of the prey (Floyd et al. 1978).

RESULTS

Habitat Use

From January to April, caribou used primarily high elevation forests (Fig. 2, Table 1). During this period, moose were located at low elevations in shrublands and riparian forest types (Fig. 2, Table 1). Wolves were also found at low elevations in habitats being used by the moose (Fig. 2, Table 1). Therefore, there was little or no overlap between caribou and wolves during this winter period.

In May, some caribou moved to lower elevations to feed on new forage production whereas others remained at high elevations. By June, most caribou had returned to higher elevations. Caribou remained primarily at high elevations in alpine and subalpine habitats throughout the summer months.

In Wells Gray Park, most caribou migrated up to 50 km. from winter ranges in highland topography to summer ranges in the Cariboo Mountains (Fig. 1). There was no distinct migration at Quesnel Lake and most of the caribou lived in highland areas throughout the summer. The migration of the Wells Gray caribou to the Cariboo Mountains resulted in them using higher elevation habitats in summer than the Quesnel Lake caribou (Fig. 2).

In summer, the moose moved to higher elevations and used subalpine forests and wetland complexes. Wolves used both high elevation and low elevation habitats in summer. Therefore, at Quesnel Lake, there was substantial habitat overlap between caribou, moose and wolves in summer. However, in Wells Gray Park,

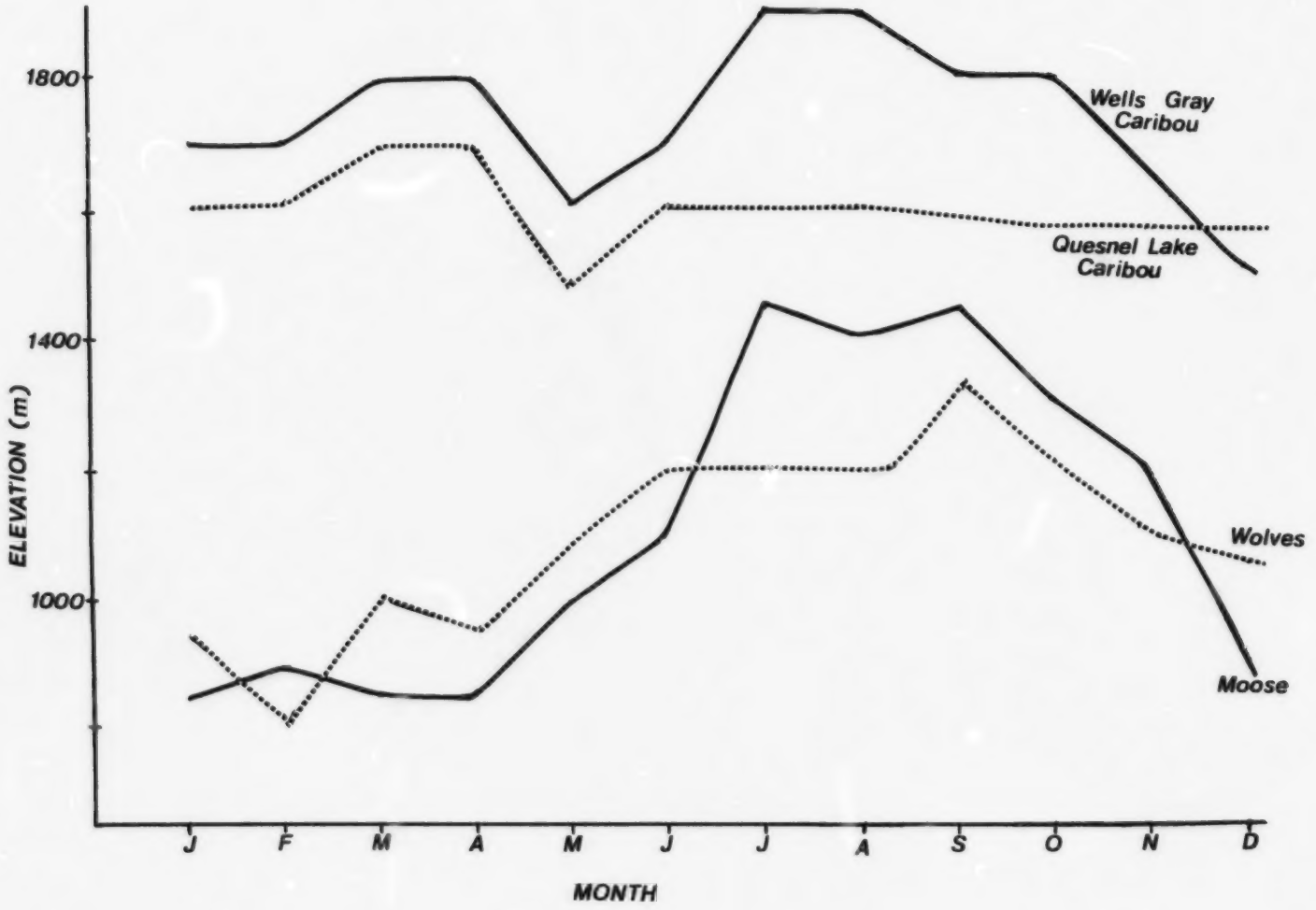

Figure 2. Mean elevation use of caribou, wolves and moose in the Quesnel Lake - Wells Gray Park area.

Table 1. Seasonal habitat use of caribou, moose and wolves in the Quesnel Lake - Wells Gray Park area.

Season/Species	# Locations	% of Locations in	
		Subalpine forests and Alpine	Low elevation forests and shrublands
January-April			
caribou	535	95	5
moose	138	0	100
wolves	50	0	100
June-October			
caribou	788	92	8
moose	71	77	23
wolves	116	33	66
November-December			
caribou	228	77	23
moose	46	0	100
wolves	22	4	96

there was little overlap between the range of caribou and wolves in summer because of the use of higher elevations by the caribou.

In early winter (Nov.-Dec.), most caribou remained at high elevations although some used lower elevation cedar-hemlock forests. The Wells Gray caribou migrated to their winter ranges at this time of the year. Moose moved to lower elevation winter ranges in November. Wolves were found primarily at lower elevations in habitats used by moose. Therefore, only those caribou which used low elevation forests in early winter were in contact with wolves.

Caribou Population Parameters

At Quesnel Lake, 19 radio-collared caribou died in 67 caribou-years of monitoring for an annual adult mortality rate of 28%. Wolf predation was the major cause of adult mortality but bear predation and accidents were also important (Table 2). In Wells Gray Park, 5 caribou died in 50 caribou-years of monitoring for an annual mortality rate of 10%. Only one case of wolf predation on a radio-collared caribou occured (Table 2).

Bear predation on caribou occured primarily in May and June when caribou and bears were using similar habitat types such as avalanche chutes and riparian areas. Wolf predation on adult caribou occured in the summer and fall when wolves were at high elevations or caribou used low elevation habitats. There were no cases of wolf predation on collared caribou at high elevations in winter. The average elevation of wolf killed caribou (X=1306 m, SD=430) was lower than the average elevation used by caribou throughout the summer (Fig. 2) indicating that caribou were more vulnerable to wolves when they were at lower elevations.

Calf survival at Quesnel Lake was very low in years when wolves were known to be present in the area (Fig. 3, Table 3). However, in the winter of 1985, the radio-collared wolf pack crossed the ice on Quesnel Lake and left the western half of the study area with few or no wolves throughout the following summer. The absence of wolves was supported by the lack of wolf scats and sign on logging roads in the area. The absence of wolves corresponded to greater calf survival in that area compared to the east side of the lake where wolves were present (Fig. 3, Table 3).

In 1987, four adult female wolves were shot on the east side of Quesnel Lake. A radio-collared male wolf and at least one associated wolf belonging to that pack moved out of the Quesnel Lake area to the east side of Wells Gray Park. This reduction in wolf numbers on the east side of Quesnel Lake appeared to result in increased caribou calf survival until August (Fig. 3).

Table 2. Causes of mortality for radio-collared adult caribou.

Cause	Quesnel Lake	Wells Gray Park
Wolf predation	8	1
Bear predation	2	3
Accidents	3	0
Malnutrition/disease	3	0
Unknown	3	1
TOTAL	19	5

Table 3. March caribou calf recruitment counts.

Year		Quesnel Lake # counted	Quesnel Lake % calves	Wells Gray Park # counted	Wells Gray Park % calves
1985	wolves present	118	7.6	0	-
1986	wolves present	65	0	0	-
	wolves absent	118	18.6		
1987	wolves present	155	9.0	221	17.7
1988	no wolf control	51	4.0	181	13.0
	wolf control	38	8.0		

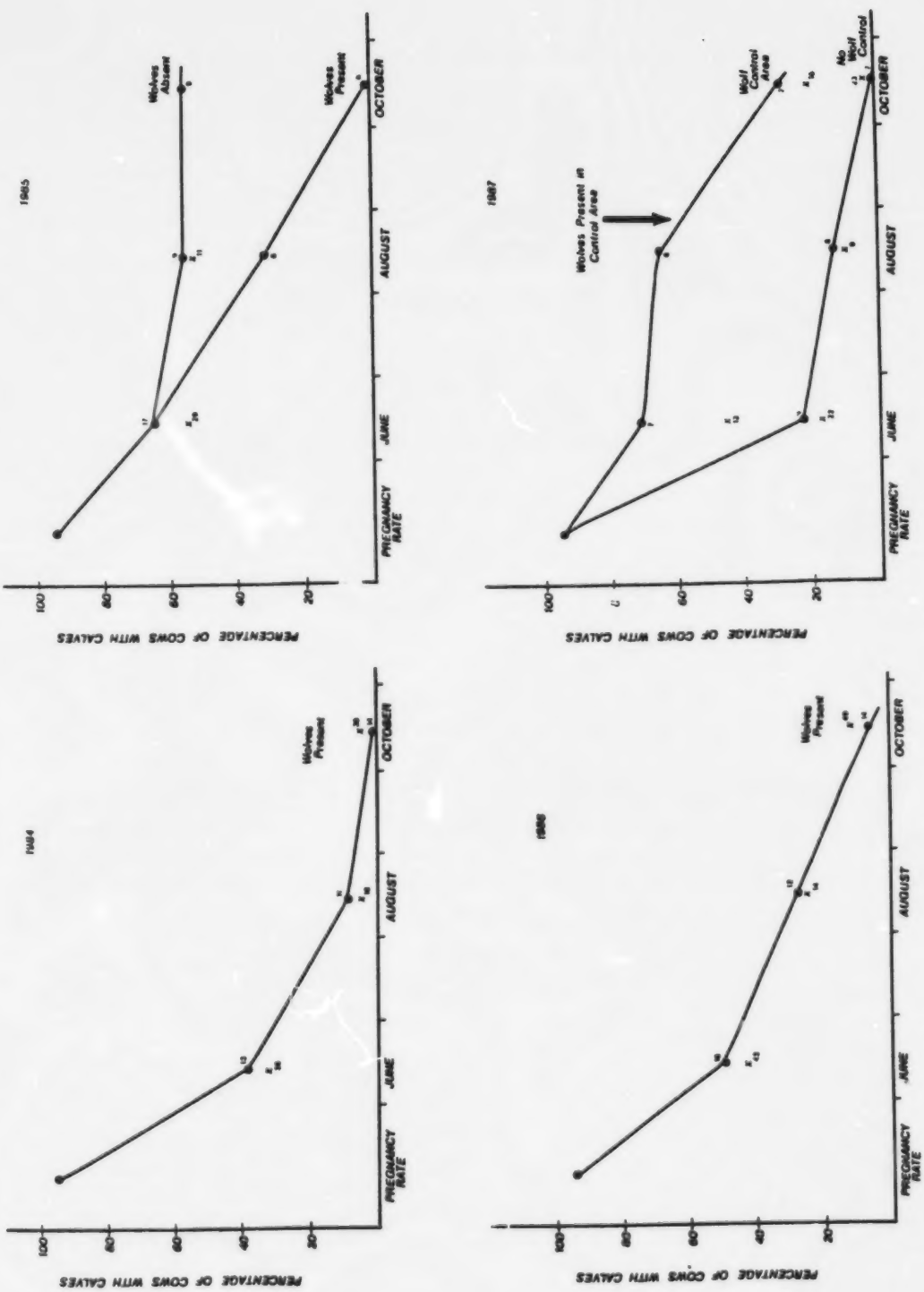

Figure 3. Percentage of caribou cows with surviving calves at Quesnel Lake. ● = radio-collared cows, x = all cows seen. Sample sizes (number of cows) are indicated.

However, wolves moved back into the area in early fall and killed a radio-collared caribou. A decline in calf survival corresponded to the return of wolves to the area and by March, calf recuitment was low (Table 3).

Calf survival in Wells Gray Park was much higher than at Quesnel Lake despite the presence of wolves in the park (Fig. 4, Table 3).

Wolf Food Habits

Scat analyses indicated that moose constituted the primary prey of wolves in summer and winter (Fig. 5). Caribou hair was found only in summer wolf scats.

DISCUSSION

The results support the hypotheses:

1. Wolf predation was a major limiting factor of the caribou population (at Quesnel Lake).

2. The wolf population was sustained primarily by moose.

Moose constituted the majority of the diet of the wolves throughout the year and the movements and habitat use of the wolves closely followed the movements and habitat use of the moose. Before the colonization of central British Columbia by moose, areas of caribou habitat in the Quesnel Lake - Wells Gray Park area probably supported very few wolves. The high snowfall and lack of available prey in these areas would make it very difficult for wolves to survive in winter if there were no moose. Mule deer (Odocoilus hemionus) migrate out of these areas to winter ranges with much less snow. Caribou and mountain goats (Oreanmnos americanus) use high elevation habitats and are largely invulnerable to wolves during the winter period. However, colonization of central British Columbia by moose in the 1920's (Edwards 1956) provided an available winter food source in the valley bottoms to sustain the wolf population.

In winter, caribou were spatially separated from wolves and moose and no predation on the caribou was detected. However in summer, if moose, wolves and caribou used similar habitats, wolf predation was a major mortality factor for adult caribou and appeared to result in very low survival of calves. The extensive overlap between the three species during the summer months in the highland topography at Quesnel Lake was associated with high adult mortality and low calf survival for the caribou. High wolf numbers were not necessary for wolf predation to be an important

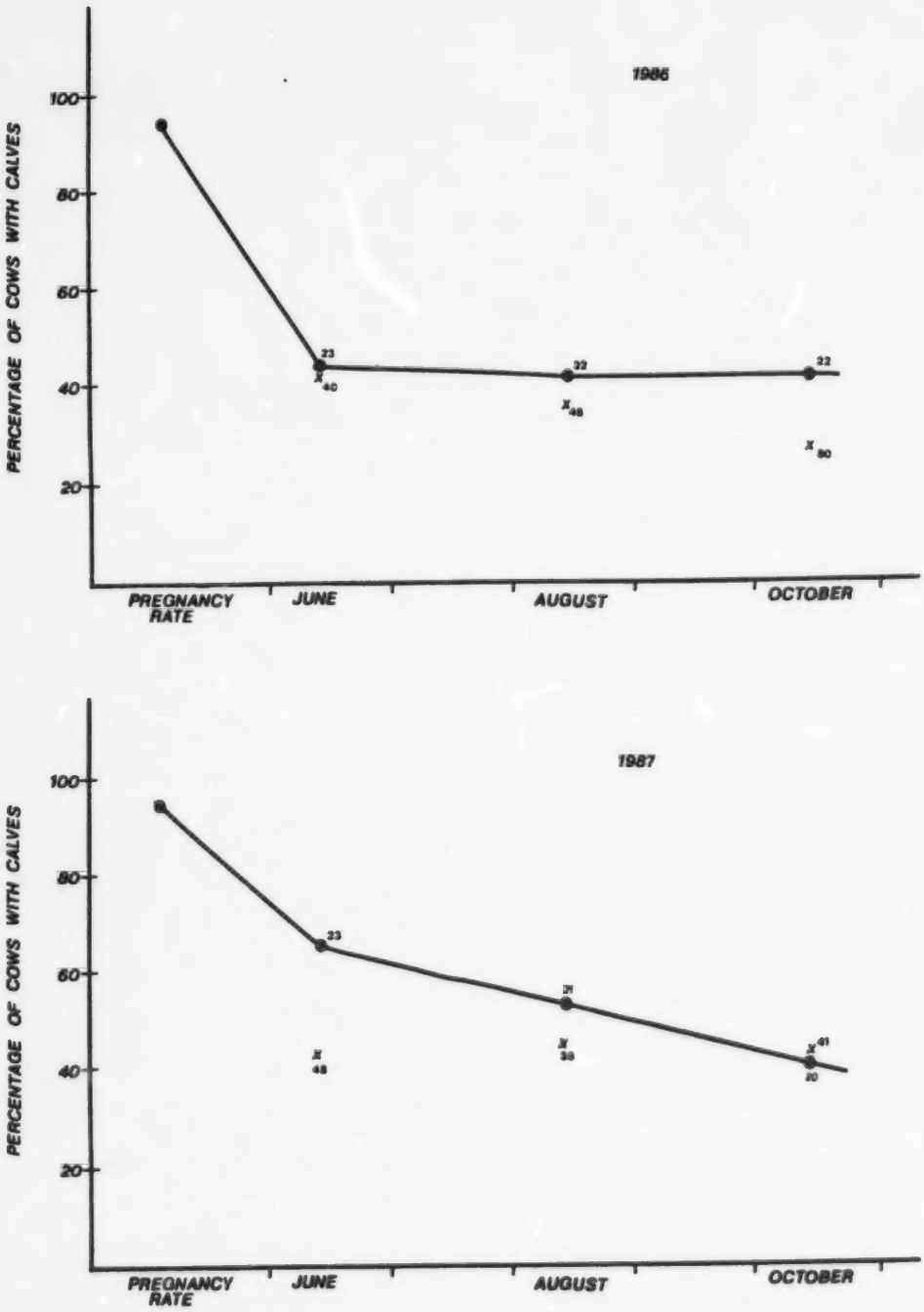

Figure 4. Calf survival in Wells Gray Park. ● = radio-collared cows, x = all cows seen. Sample sizes are indicated.

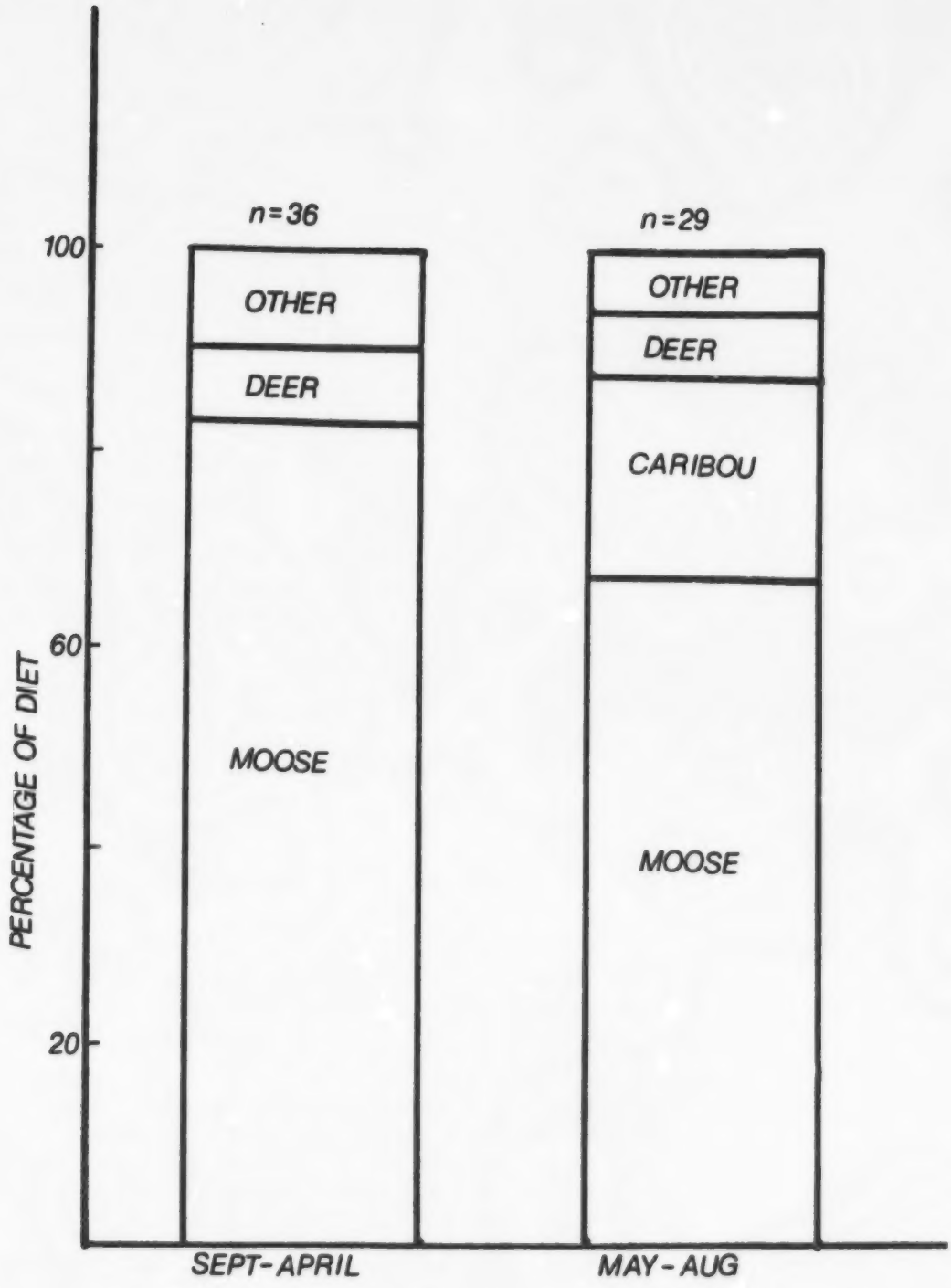

Figure 5. Food habits of wolves in the Quesnel Lake area based on scat analysis.

limiting factor. It appeared that a wolf population of less than 15 wolves (1 wolf/175 km) was responsible for the high predation rate on the 150-200 caribou at Quesnel Lake. The high level of predation at Quesnel Lake was causing a decline in the caribou population and potentially would have caused the extirpation of caribou from the area in the near future. A wolf control program was intiated in 1987 to improve caribou survival rates and prevent the extirpation of the caribou. This program is being monitored to evaluate the effect on the caribou population.

In Wells Gray Park, caribou survival rates were much higher than at Quesnel Lake and the population was probably slowly increasing. The lower wolf predation on the caribou in the park may have been due to the increased spatial separation between caribou and wolves/moose that occured because of the migration of the caribou to high elevation, rugged mountains for the summer.

In summary, the colonization of central British Columbia by moose appears to have resulted in the maintenance of increased wolf populations in areas of caribou habitat. Moose were the primary food of the wolves and the movements of wolves were closely tied to the movements of the moose. Wolf predation was a major limiting factor for the caribou population in the Quesnel Highlands area in which there was extensive overlap between caribou, moose and wolves for much of the summer. Predation could possibly extirpate caribou from these highland areas. However, in more rugged mountains, spatial separation between caribou and wolves in summer may allow caribou, moose and wolves to co-exist.

MANAGEMENT IMPLICATIONS

1. In highland areas such as Quesnel Lake where caribou, moose and wolves extensively overlap on summer ranges, wolf control appears to be required to maintain caribou populations.

2. In Wells Gray Park, migration of the caribou to high elevation summer ranges results in spatial separation between caribou and wolves and may explain the lower predation rate on the caribou. If so, wolves, moose and caribou should be able to co-exist without wolf control.

3. Enhancement of moose populations can potentially lead to increased wolf numbers and an increased predation rate on caribou. Therefore, habitat enhancement for moose in areas of caribou habitat should be approached with caution.

ACKNOWLEDGEMENTS

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WOLF/PREY STUDIES IN THE YUKON TERRITORY, 1983-88

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INTRODUCTION

The systematic study of Yukon wolves (Canis lupus) was initiated in 1983 in response to moose (Alces alces) and woodland caribou (Rangifer tarandus) population declines, and a perceived increase in wolf numbers in the southern Yukon (Hayes et al. 1985). Prior to 1983, little was known of Yukon wolf ecology or population dynamics. Wolf management programs in the 1950's and 1960's involved the use of poisons to increase game populations in various Yukon areas (Smith 1983). The effects of poisoning on wolf numbers, and on ungulate population responses were not monitored.

This paper reports on various wolf/ungulate studies (Figure 1, Table 2) that have been conducted since 1983, including two controversial wolf control programs aimed at increasing moose and caribou populations in the southern Yukon. Study results are summarized here; comprehensive accounts are found in various Yukon Fish and Wildlife Branch reports (Table 1).

STUDIES

COASTAL MOUNTAIN WOLF STUDY

A moose population decline and low calf survival rates since 1981 (Larsen 1982; Johnston and McLeod 1983; Markel and Larsen 1983) prompted wolf studies in January 1983, in the Coastal Mountains (Figure 1) southwest of Whitehorse (Hayes et al. 1985). Studies included systematic annual wolf inventories (1983-1988) and radio-telemetry studies of a total of 60 instrumented wolves between 1983 and 1987 (Hayes et al. 1985; Hayes and Baer 1986; Hayes, unpubl. data). Concurrent moose population research included population surveys and a mortality study of radio-instrumented cow and calf moose (Gauthier and Larsen 1986; Larsen and Gauthier 1986; Larsen et al. 1987).

Moose studies showed that annual cow survivorship was high (91%) and was not affected by wolf density changes. Calf survival averaged 25% from 1983 to 1985. Of the radio-instrumented calves that died, 92% were killed by predators; 58% were killed by grizzly bears (Ursus arctos), and 25% were killed by wolves. Considering all known causes of mortality in the moose population, Larsen et al. (1987) concluded the relative importance among major causes were as follows: grizzly bear 50%, wolf 26%, and hunting 9%. The important management implications of their research were:

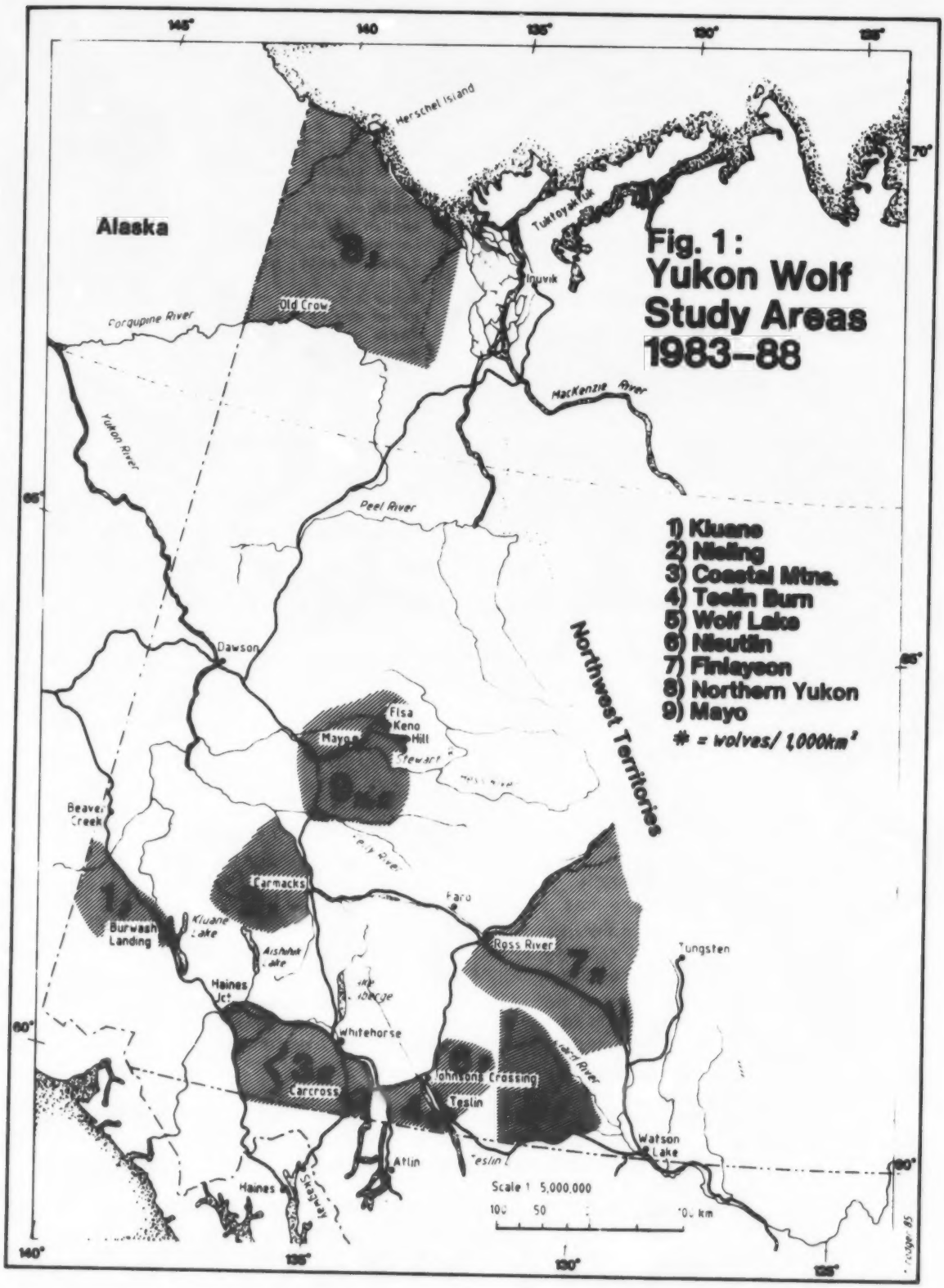


Fig. 1: Yukon Wolf Study Areas 1983–88

Table 1. Wolf-prey studies in the Yukon Territory, 1983-88

Project	Duration	Study Area sq km	Reports
Coastal Mtns.	1983-88	13,140	Hayes et al 1985 Hayes and Baer 1986 Hayes unpubl. data Gauthier and Larsen 1986 Larsen and Gauthier 1986 Larsen et al 1987 Larsen unpubl. data
Finlayson	1983-92	24,000	Farnell and McDonald 1987 Hayes and Farnell 1985 Hayes and Farnell 1986 Hayes unpubl. data
Wolf Lake	1985 1988	6,100 12,500	Hayes and Bowers 1987 Hayes unpubl. data
Nisutlin	1987	4,970	Hayes and Baer 1987
Nisling	1986 1988	4,045 7,500	Baer and Hayes 1987 Hayes unpubl. data
Teslin Burn	1984	2,580	Hayes and Baer 1986
Mayo	1988	13,000	Hayes unpubl. data
N. Yukon	1986-91	40,000	Hayes and Barichello 1986 Hayes et al 1988
Kluane	1985-86	9,770	Sumanik 1987

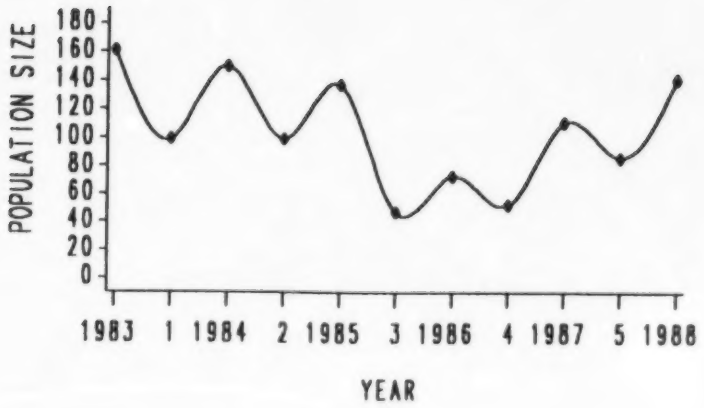
1. Because grizzly bears are not obligate carnivores, their demographics are not regulated by changes in moose population demography. Grizzly bears could limit moose calf survival for extended periods due to the absence of predator/prey feedback mechanisms.

2. The use of wolf/prey ratios should be carefully assessed, and cautiously used, in areas where grizzly bears and wolves both occur.

3. If combined predator reductions are to increase moose, managers need to first consider both inter-specific and intra-specific compensation among predators.

4. The management problems associated with moose/grizzly bear-wolf systems are limited to the Yukon, Alaska and parts of British Columbia, Alberta, and the Northwest Territories (Larsen et al 1987).

FIGURE 2. COAST MOUNTAIN WOLF POPULATION SIZE, 1983 – 1988



1,2,3,4,5 REPRESENT LATE WINTER WOLF NUMBERS

In the Coastal Mountain study area, efforts to increase moose numbers included the relaxation of bear hunting regulations and the opening of previously closed outfitting areas to non-resident hunting. Few bears were eventually removed from the study area (Larsen unpubl. data).

Wolf control using government aerial hunting was initiated in 1984 when a 44% removal of wolves was achieved (Figure 2). By April 1985, after three years of wolf control, 70% of the original wolf population was killed. Following the cancellation of wolf control in 1985, continued research over three years documented wolf population recovery in the area. Wolf population size increased since 1985 to a level of 140 wolves in 1988 (Figure 2); representing a recovery to 88% of the original population size (160 wolves). Wolf demographic studies were completed in 1988, and are presently being summarized (Hayes unpubl. data).

Late winter wolf predation rate studies were conducted in 50-60 day study periods during 1984 (Hayes and Baer 1986) and 1986 (Hayes unpubl. data). Early winter predation rates were studied during a 30 day period in 1986 (Hayes unpubl.

data). Results showed that moose were the most important prey species of most studied packs. Certain packs also hunted Dall's sheep (Ovis dalli). Rates of predation and consumption in four study packs monitored in 1984 were similar to other studies where moose were the primary prey (Hayes and Baer 1986). Predation rates of nine wolf packs were measured during the early recovery phase (1986) to determine the effects of reduced pack size on wolf predation and consumption rates. Preliminary data showed that moose calves were killed infrequently and represented a lower proportion of the kills compared to the proportion of calves available (Hayes unpubl. data). Studies of solitary wolves showed they were capable of killing calf and yearling moose, and Dall's sheep rams.

FINLAYSON CARIBOU MANAGEMENT AREA

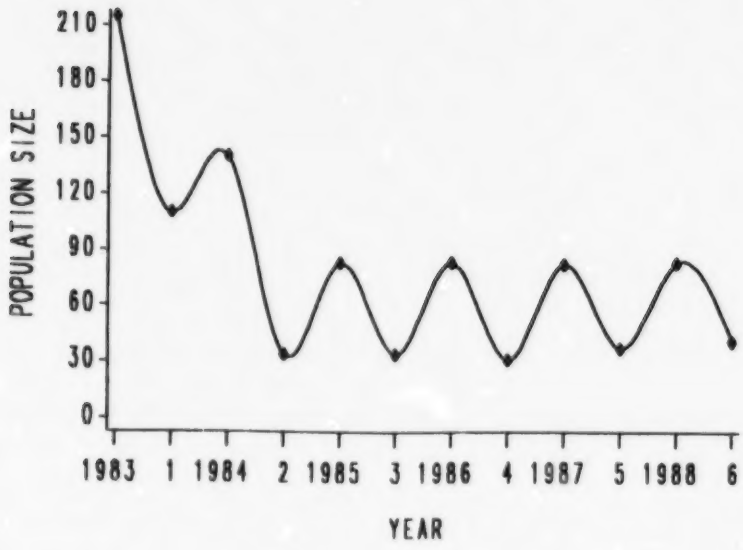
In 1982, Farnell and McDonald (1987) documented population problems in the Finlayson woodland caribou herd in the east-central Yukon (Figure 1). The mean calf percentage was 9.8% and annual harvest, largely native subsistence, was 250 animals; about 10% of the herd. They predicted the herd was decreasing by 11% annually. In an attempt to reverse the decline, three techniques were employed to reduce caribou mortality: sport hunter kill was restricted to male caribou only; native subsistence kill was shifted from females to males, and voluntarily reduced; and, using aerial hunting techniques, the annual regional wolf population was severely reduced over a 6 year period (1983-88). Studies of control effects on wolf population status are found in Hayes and Farnell (1985; 1986; unpubl. data).

The percentage of calves in the herd increased from 9.8% in 1982 to 14.9% in 1983, following a 49% reduction in wolf numbers. Since 1984, when wolf reductions exceeded 84% of original levels, the percentage of calves in the fall population averaged 20% (Farnell and McDonald 1987). Mortality rates of radio-instrumented adult caribou also declined dramatically in response to the management program, from a high of 27% in 1982 to about 11% since 1984 (Farnell and McDonald 1987).

By using radio-cesium 137 techniques on wolf skeletal muscle tissue (Holleman and Stephenson 1981), we were able to determine wolf winter predation patterns in the study area. Cesium data showed that wolves killed on caribou winter range relied heavily on caribou as prey. Wolves mainly preyed on moose in other portions of the study area.

Jingfors (1988) conducted a moose survey in the Finlayson area in 1987. He suggested that the high proportion of calves (64-69/100 cows) and yearlings (54-56/100 cows) indicated an increasing moose population, and that the timing

FIGURE 3. FINLAYSON LAKE WOLF POPULATION SIZE 1983–1988



X AXIS INTEGERS 1,2,3,4,5,6 REPRESENT LATE WINTER WOLF NUMBERS

and extent of moose population growth was likely a response to Finlayson wolf control.

Figure 3 shows the wolf population trend since 1983. Since 1985, the annual rate of recovery has ranged around 2.5. This rate is high compared to Keith's (1983) average of 1.29 calculated from seven previous control programs. This can be explained by the high proportion of wolves annually shot (>80%). At exceptionally low wolf density, the demographic importance of a new wolf is proportionally greater than at higher densities. For example, the addition of 10 new wolves into a remnant population of 10 will double the population. The rate of increase will be 2.0. Ten wolves into an existing population of 40 will produce a rate of increase of only 0.80. Since 1984, the annual surviving population was about 40 wolves. By the following late winter, after natural mortality factors undoubtedly removed some wolves, the population size exceeded 80 wolves. These trend data show that, despite exceptionally high annual removal rates, the ability of wolves to annually repopulate the area was not negatively affected, as recovery rates have been the same since 1984 (Figure 3). These population recovery fea-

tures were likely due to the large, naturally-regulated wolf population surrounding the wolf control area.

After March 1989, wolf control will be completed, making this one of the the longest (7 years), most annually intensive wolf control program in North America.

WOLF LAKE WOLF STUDY

An important component of the Finlayson program has been monitoring the effects of wolf removal on an adjacent wolf population. Wolf population inventories were conducted in the Wolf Lake area (Figure 1), immediately south of the Finlayson wolf removal area (Figure 1) in 1985 (Hayes and Bowers 1987), and 1988 (Hayes and Baer unpubl. data). Results from 1985 showed that Wolf Lake wolf density was 9-11 wolves/1000 sq km, compared to 4.6 wolves/1000 sq km at Finlayson, following three years of wolf control. The Wolf Lake density was similar to the density found at Finlayson prior to wolf control in 1983. This suggested there was no negative effect on wolf distribution and density in Wolf Lake due to wolf removal in the Finlayson study area.

A subsequent survey in 1988 showed wolf density was lower than 1985, at 7 wolves/1000 sq km. Few wolves were seen in the northern portion of the study area, where two large packs ranged in 1985. It is known that a pair of wolves that ranged mainly in the Wolf Lake area in 1988 was shot while in the Finlayson control area, and it is likely that in other years, bordering wolves were also removed. The observed decline in density from 1985 to 1988 showed that wolf control in Finlayson also was depressing wolf numbers immediately outside the southern boundary of the Finlayson removal area. However, the effect apparently was local to the border area, for wolf distribution and density in the remainder of the Wolf Lake study area did not change between 1985 and 1988 (Hayes unpubl. data).

WOLF POPULATION INVENTORIES

To gain a better understanding of wolf distribution and density, and the potential effects wolves have on regional ungulate populations, a wolf inventory was designed to follow regional moose and caribou population inventories throughout the Yukon. To date, four ungulate survey areas have been concurrently censused for wolves (Figure 1): the Nisutlin River (Hayes and Baer 1987), the Teslin Burn (Hayes and Baer 1986), the Nisling/Casino Trail area (Baer and Hayes 1987; Hayes and Baer unpubl. data) and the Mayo area (Hayes and Baer unpubl. data).

Data from all areas where wolves have been censused show a wolf density range of 3-18 wolves/1000 sq km. In the southern Yukon, most areas support wolf densities of 8-12 wolves/1000 sq km. The lowest density recorded was 3.2 wolves/1000 sq km in the Nisling River (Baer and Hayes 1987). Recent moose surveys (Markel and Larsen 1988) showed that this area also supported the lowest recorded moose density in the southern Yukon (40/1000 sq km).

THE NISLING WOLF/WOOD BISON STUDY

In spring 1985, a small herd of 34 wood bison (Bison bison athabaska) were transported from Elk Island National Park, Alberta and released within a large holding compound on the upper Nisling River. In March 1988, 22 animals were released. A wolf population survey was completed in 1985 (Baer and Hayes 1987) and 1988 (Hayes unpubl. data) (Figure 1) to monitor wolf distribution and density in the area. Plans for 1988-89 include radio-instrumenting wolves from a known pack of seven that range near the compound to determine their movements and behaviour in relation to the bison herd. To date, no wolf predation has occurred.

NORTHERN YUKON WOLF STUDY

A comprehensive study of wolves in the northern Yukon was initiated with a wolf den survey in 1986 (Hayes and Barichello 1986), followed by a systematic inventory and radio-telemetry study of wolf movements, distribution, prey relationships and wolf mortality in a 39,600 sq km area in 1987 (Hayes et al 1988, Figure 1). Wolf density was 3.1 wolves/1000 sq km, with the highest concentration of wolves in the Richardson Mountains. A total of 28 wolves were radio-instrumented in 13 packs. First year study results showed wolves were largely non-migratory; wolves on the North Slope drainages hunted caribou and moose, while wolves on the south slopes of the Richardson and British Mountains mainly killed moose, and caribou whenever they were available.

Preliminary radio-cesium data from 15 wolves shot near Aklavik in 1987 (P. Clarkson unpubl. data) showed light use of caribou, although a few thousand caribou wintered in the same area. In 1988, the majority of the 165,000 caribou in the Porcupine herd wintered in the study area. In an attempt to assess whether migratory wolves had moved into the study area in association with the herd, an additional 11 wolves were radio-instrumented in April, 1988. Planned activities include monthly monitoring of radio-instrumented wolves in relation to local moose (Smits 1988), and international caribou studies. Data from this work will provide a more comprehensive understanding of the role wolves play as

furbearers to Inuvialuit hunters and trappers, and predators of large ungulates in the northern Yukon.

WOLF/DALL'S SHEEP STUDY

R. Sumanik (M.Sc. thesis 1987) studied wolf/Dall's sheep relationships in the Kluane area in 1985 and 1986 (Figure 1). Following a total of 14 radio-instrumented wolves in 7 packs, he concluded that all wolf packs ranging in alpine sheep habitat hunted and killed sheep. Some packs relied entirely on sheep during the winter, and Kluane wolf predation rates were low compared to other North American wolf studies. He also concluded that wolves in Kluane were characterized by low density, small packsizes, large territories, high human-caused mortality, low productivity, and frequent dispersal.

In his sample of wolf-killed sheep, Sumanik concluded that wolves did not select for certain sex or age class. Hayes (unpubl. data) also observed this characteristic from 30 sheep kills studied in the Coastal Mountains. Wolves in Kluane appeared to select sheep only when moose and caribou prey were scarce in their territories. Sumanik's study did not support Murie's (1944) Denali National Park, Alaska study, that concluded wolves were limiting sheep population growth. Alternatively, Sumanik (1987) suggested that the reliance on sheep for primary prey appears to be limiting wolf colonization in Kluane.

WOLF EDUCATION/INTERPRETATION

Since 1986, the wolf management program has cooperated in the University of British Columbia Environmental Education Course, instructed by R. Jickling. The focus of our cooperation has included visits to an active wolf den. Additionally, as part of the wilderness canoeing component of the course, the first author has engaged in wolf howling as a method for engaging wolves in the wilderness, and lectured on wolf biology and management to students.

FUTURE STUDIES

The priorities for continuing wolf research include:

1. The completion of the northern Yukon wolf study (1990).

2. Further development of wolf population inventories as an integral component of regional ungulate management plans.

3. Completion of Finlayson wolf control (1989) and initiation of wolf population recovery studies (1989-92). A unique opportunity exists to investigate wolf recovery parameters of a severely reduced wolf population into an enriched caribou and moose prey base. Questions to investigate include: Will the wolf population recovery rate be affected by the long-term, intensive removal there? Will wolves achieve densities greater than those prior to wolf reduction, in response to the increased size of the prey base? Is there a multiple equilibrium between northern wolf and prey populations (Farnell and McDonald 1987)?

4. Continued development of educational and interpretive uses of wolves.

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Wolves in Riding Mountain National Park: Ecosystem protection and thoughts on a holistic conservation strategy

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Historical Background

One hundred years ago, Riding Mountain National Park was simply an escarpment that blended into the surrounding landscape. Wolves, grizzlies, and their prey - elk, moose, beaver, and deer - were free to roam through boreal forests that alternated with aspen forests and prairie landscapes. There were no boundaries; it was all part of a vast wilderness area. These conditions began to change when Europeans settled the region in the latter part of the 19th century. Land was cleared around the escarpment; this process threatened the mammal populations within the area. Fortunately the wisdom of some enlightened authorities prevailed; by 1895 the escarpment was withdrawn from settlement, and in 1906 an official Forest Reserve was established. In 1929, the area was set aside as a National Park, then was officially declared as such in 1933. In 1986, the park and surrounding agricultural areas were declared a Man and Biosphere Reserve.

During this time, and continuing until today, clearing of the land has drastically modified the landscape around the park. The escarpment has become isolated from its surroundings (Figure 1) and is now a separate biogeographic entity. Functionally, the park is now an island - not in the sense of land surrounded by water, but in much the same way that MacArthur and Wilson (1967) suggested that terrestrial environments such as caves or mountain tops may function as islands. The Biosphere Reserve consists of the park - a core of approximately 3000 km^2, and a surrounding agricultural area of approximately 6700 km^2 (Figure 2).

The "Man and Biosphere" (MAB) program is an outgrowth of the 1968 Biosphere Conference, which was convened in Paris by UNESCO and several U.N. agencies (Francis 1988). Today, more than 100 countries participate in this program. The emphasis is on management-oriented ecological research and on environmental monitoring that centres on the preservation of core areas and the sustained use of resources in adjoining areas.

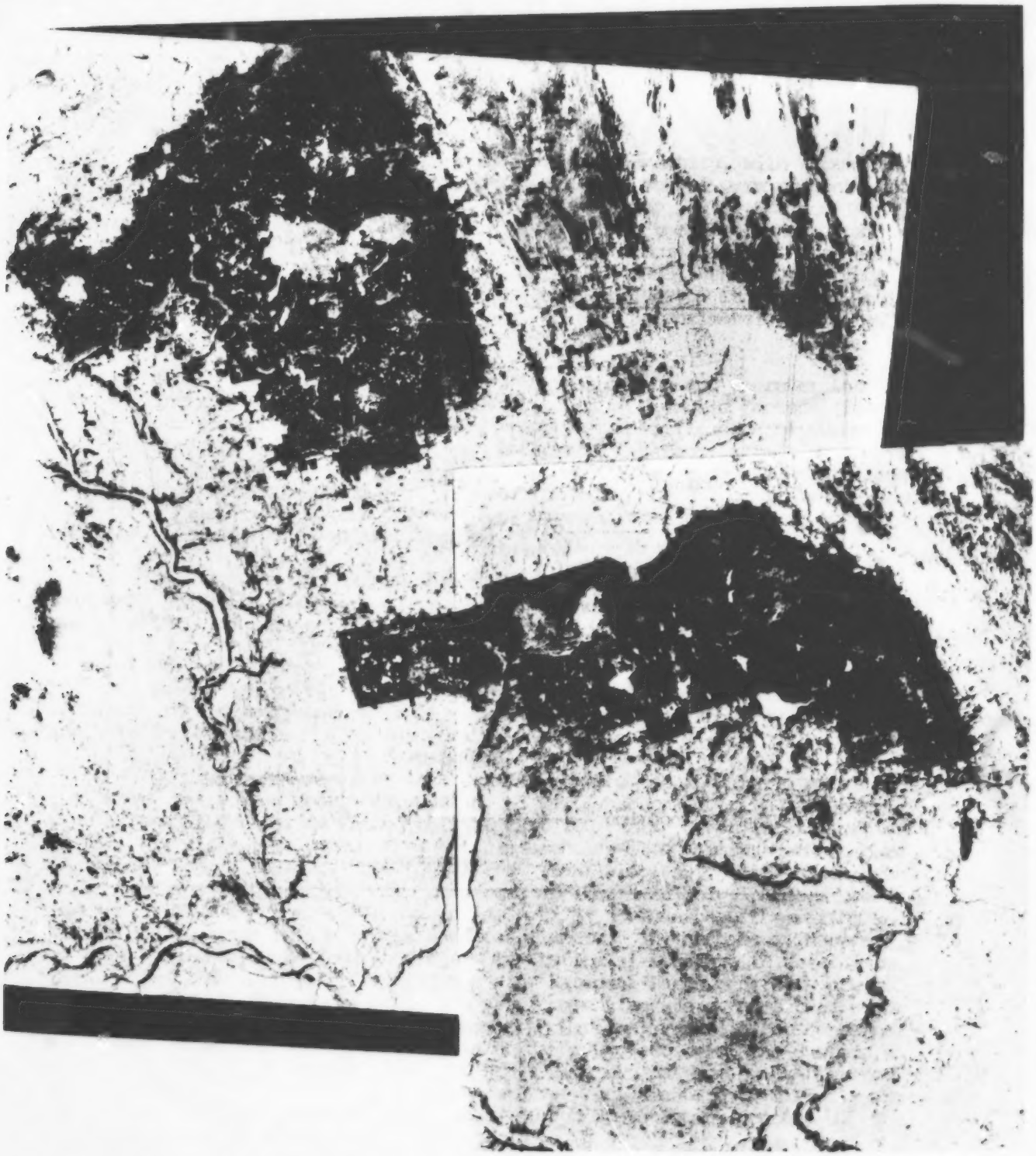

Figure 1. Aerial view of Riding Moutain National Park (lower right) separated from Duck Mountain Provincial Park by approximately 35 km . Both parks have become isolated forest reserves, surrounded by agricultural areas.

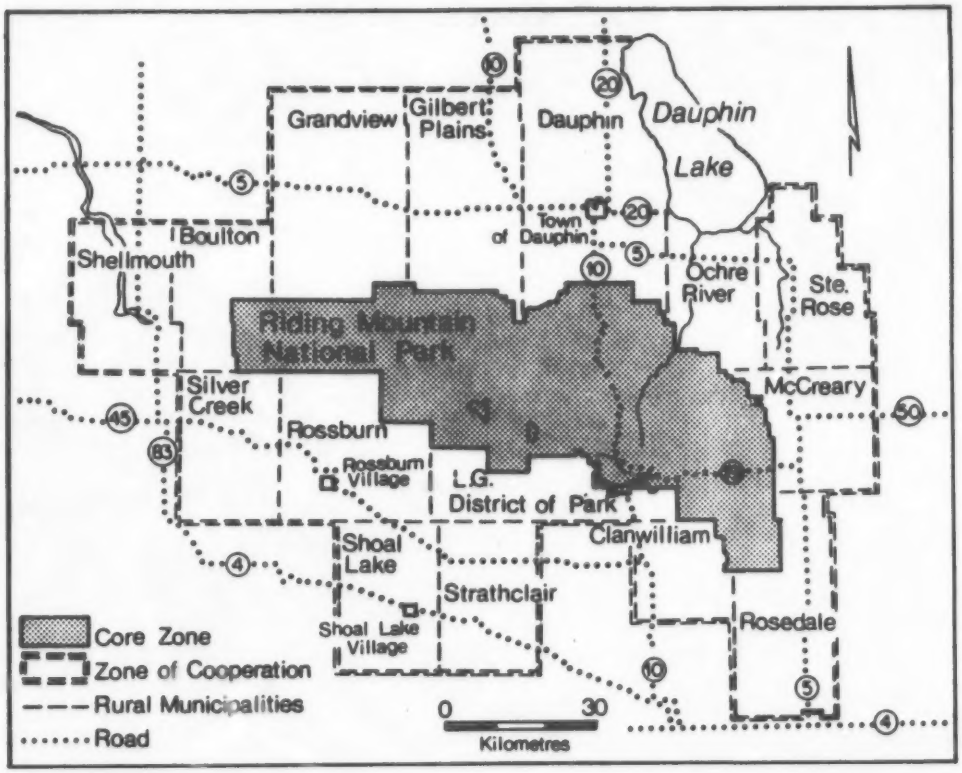

Figure 2. Riding Mountain National Park, Man and Biosphere Reserve was established in 1986 and includes the park (core zone - 2978 km^2) and 18 municipalities (zone of cooperation - 6700 km^2).

Like all ecosystems, the park is a dynamic entity, with a constant ebb and flow of the components within (Figure 3). Wolves were present when settlers first homesteaded in the region (Wrigley 1979, Stardom 1983). Predator control programs and more intense farming resulted in elimination of the wolves by the turn of the century (Stardom 1983). In the early 1930's, wolves recolonized the area (Soper 1940, 1953); this event roughly followed major increases in elk numbers (Banfield 1949). It is likely that wolves moved in from the Duck Mountains, an area approximately 35 km north of the park (Figure 1).

Man's relationship to wolves, in this region and wherever the two species interact, is, and has often been, based on economic factors (Figure 4). Under pristine conditions (i.e., prior to the settlements of Europeans in Manitoba), wolves and ungulates interacted without affecting man's economy, therefore, wolves were outside man's economic sphere. Once farming and hunting became established, wolves and man began to compete for resources, with the result that wolves were eliminated in all of southern Manitoba, except in the National Park.

Wildlife, and wilderness, attracts tourists to Riding Mountain National Park; at the same time, hunters benefit when ungulates leave the park. In this way, wolves have a positive impact on man's economic sphere. Predation on cattle (livestock) and surplus huntable ungulates by wolves has a negative impact on man's economic sphere. It could be argued that, without wolves in the park, more game would be available outside the park. We must recognize that today's balance between predator and prey may not be the same in the future.

Natural systems are not static entities, so the prey populations available to wolves have fluctuated. Elk, moose, deer [1], and beaver populations have varied throughout the last 100 years (Green 1933; Trottier et al. 1983). Following the establishment of the park, elk numbers increased to a level of "overpopulation" (Banfield 1949). Moose have been present throughout, but their numbers have increased only in recent years (Rounds 1977). From these examples, it is obvious that the waxing and waning of elements in the system has been important in the past. Therefore, we can predict that the ungulate/wolf ratios will change in the future. Changes in the wildlife populations in National Parks generally are not viewed by wildlife management in the same context as are changes that occur elsewhere. The management of resources in National Parks is not concerned with maximum production; instead, it stresses protection of the system, so that evolutionary processes can progress with minimal human interference. Nevertheless, the human presence is often very prevalent, both directly and indirectly, and can have a marked influence on evolutionary processes. The status of beaver in the park is a good example.

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[1] Currently only white-tailed deer are present; in earlier years (prior to the 1940's) mule deer prevailed in the system.

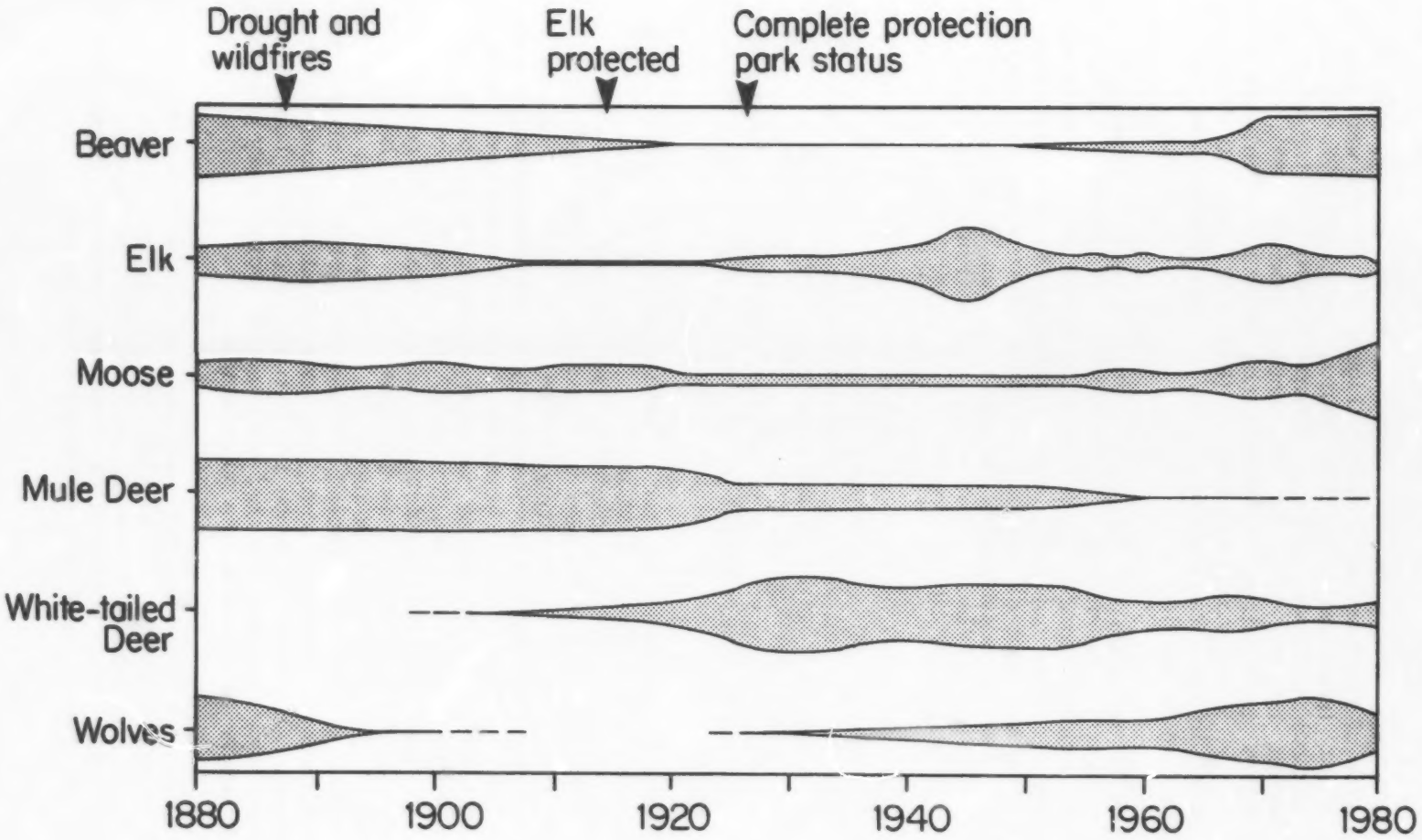

Figure 3. Diagrammatic representation of wildlife abundance trends in Riding Mountain National Park from 1880 to 1980.

Figure 4. In the past, wolves competed with man for resources; this still occurs in some areas. Only in recent decades have wolves gained a more positive relationship with man.

The aspen parkland/boreal environment in the park provides an ideal habitat for beaver. The beaver population declined with the emergence of the fur trade; this decline continued throughout the period of human settlement (Green 1936). Heavy trapping around the turn of the century is believed to have caused the decline in numbers (Green 1936), although other factors may also have been important. Beaver were not common in the 1940's; reintroductions took place in 1947 and in 1958 - by 1959, beaver were well established and their numbers continued to increase, reaching a peak (an estimated 3500 colonies) by 1979 (Trottier et al. 1983). The presence of beaver has a profound effect on habitat modification; furthermore, they may be an important buffer prey species for canids during the summer, the only time that wolves and coyotes have ready access to them.

Human hunters outside the park shoot elk, deer, and moose during the hunting seasons. The number of elk killed annually has varied from as many as 1834 (1950) to as few as 26 (1986). On the average, approximately 300 to 400 animals (roughly 10% of the park's estimated population) are shot each year, although the total numbers killed in recent years have been lower (Park files and Paquet et al. in prep.).

The research on the predator/prey system (also referred to as the Large Mammal Systems Study), in which the Canadian Wildlife Service became involved, has been divided into two phases. Phase 1 began in 1975 and continued until 1980. During this period, 23 wolves were radio-collared. Phase 2 began in 1982, with the arrival of the first graduate students, and continues today - in this phase, coyotes, as well as wolves, were studied. The emphasis was shifted from the radio-telemetry of wolves in Phase 1 to naturalistic studies and population monitoring in Phase 2. A major component throughout both phases was warden surveys of ungulates and beaver. Because of political, jurisdictional, and agency priorities, intensive research on population dynamics, using radio-telemetry of wolves inside the park, has not been carried out since 1980. Since then, the wardens have been responsible for the long-term monitoring of changes in predator/prey population trends inside the park. Student thesis projects in the park involve naturalistic studies; outside the park they include naturalistic and radiotelemetric studies.

The material in this paper is based on information collected by many individuals, especially the park wardens, who, over several decades, have conducted aerial and ground surveys of all the major species of mammals. Space restrictions do not allow all of their reports to be quoted (2-3 reports per year) - these are on file in the Riding Mountain National Park library and at Parks Canada Regional Headquarters in Winnipeg. A summary of the information is contained in reports by Burles (1986) and Walker (1987). The methods used in these surveys are contained in the annual reports; those for ungulates are summarized in Carbyn 1983. Students Tim Trottier, Dennis Meleshko, Paul Paquet, Scott McKinlay, and Dean Cluff provided continuity between projects. A major portion of the funding came from the Canadian Wildlife Service, the World Wildlife Fund, and the Boreal Institute of the University of Alberta. Parks Canada and Manitoba Wildlife (Manitoba Natural Resources, Wildlife Branch) provided permission to carry

our the research in the park and province, respectively. Dr. Roger Edwards, Elaine Street an Ed Telfer reviewed the paper at various stages of completion. Bernie Jones typed the manuscript, Andrew Raszewski and Susan Popowich drafted the figures.

Results

The results of the long-term, on-going studies have been published elsewhere; only a brief summary is presented in this paper. Mid-winter aerial surveys from 1975 to 1979 showed mean densities of approximately 1.4 elk and 0.94 moose/km^2 (Carbyn 1983). The results of surveys subsequent to 1979 were obtained from park records (Figure 5). Sufficient data to determine the annual densities of deer are not available, but the numbers from 1975-1986 were considerably lower than for elk and moose.

The average territory size of radio-collared wolf packs was 260 km^2 (Carbyn 1983). The average overlap of territories between years was approximately 30% (Carbyn 1982). This instability probably results from the loss of wolves to outside human activities, since it is conceivable that pack disruption gives rise to changes in behavioural responses. Annual losses attributable to human activities were variable; prior to 1980 they ranged from 14% to 78% for individual packs. For the whole park, losses due to human trapping, predator control, and hunting between 1975 and 1986 accounted for about 15% of the total population. Wolf numbers were moderate and relatively stable from 1975 to 1986 (Figure 5). Since the average mortality that was directly attributable to losses when the wolves left the park was low, other factors must be considered as posible regulators of wolf numbers. The two most likely factors are a low reproductive rate and a high rate of natural mortality in the park - either litter sizes were small or mortality due to natural causes was high. On the basis of the incidence of disease recorded within the wolf population (distemper and tuberculosis), it can be surmised that disease may be an important factor in mortality. Since the publication of the paper on disease in wolves in the park (Carbyn 1982), another disease, the canid parvo-virus, has been found in both wolves and coyotes (unpublished data).

Late-winter pack size ranged from 5 to 10 ($x = 6$ wolves per pack). Packs of 16 or more animals were present only in 1975, the first year of study.

Mid-winter ungulate/wolf ratios for the two packs that were studied in the winter of 1978/79 were 131 elk, 54 moose, and 24 deer/wolf (Carbyn 1983). The predation patterns observed over the years clearly indicate that the major prey species is elk, which represents approximately 65% of winter kills. Deer represent approximately about 15 - 20% of the kills and moose about 10 - 15%. Wolf kills contain a higher percentage of young animals than do recreational kills of elk by humans; the latter contain larger numbers of mid-aged (2-6 year old) elk (Carbyn 1983). The examination of wolf scat samples indicates that beaver are an important prey species during summer (Meleshko 1986).

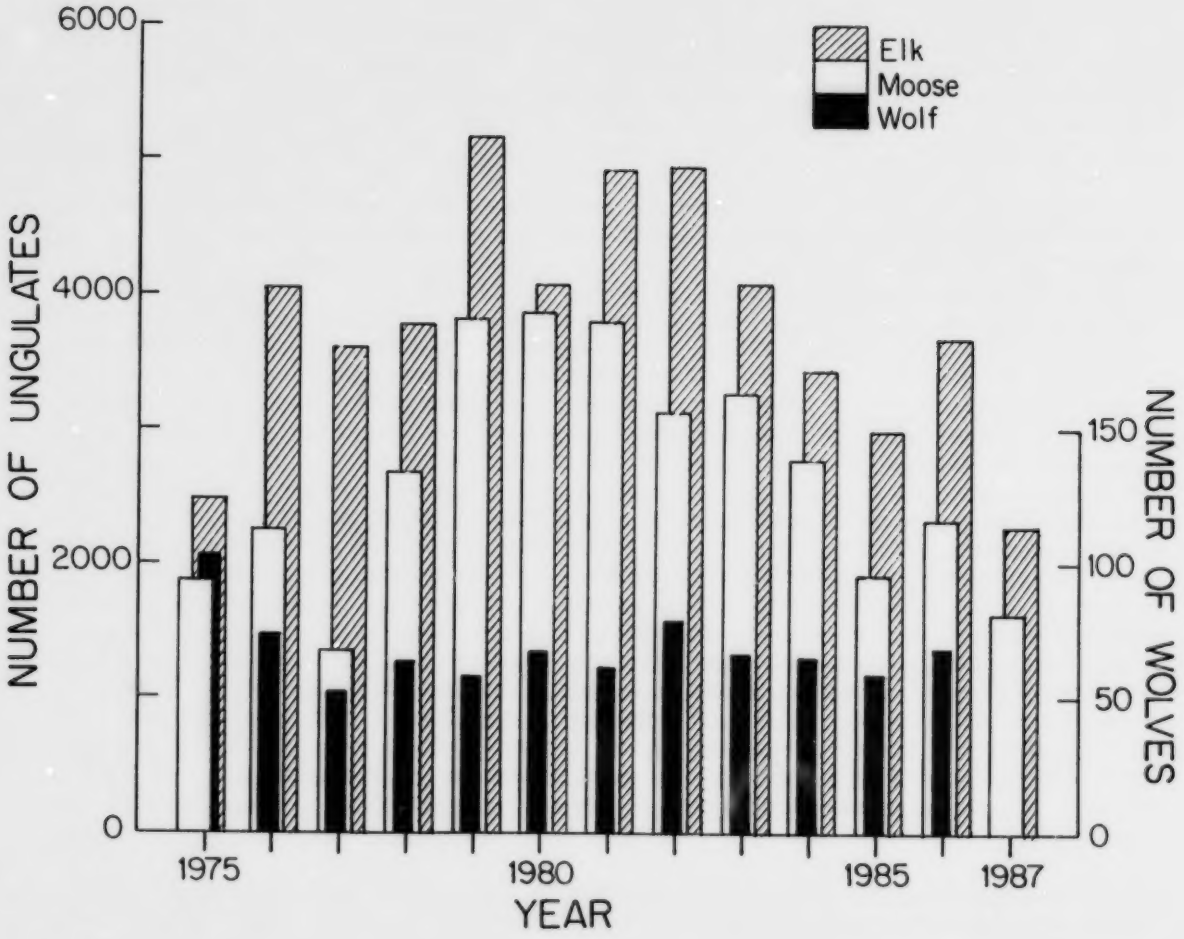

Figure 5. Elk, moose, and wolf population trends, as obtained from annual park surveys carried out from 1975 to 1987 by Park wardens and Canadian Wildlife Service personnel.

Most of the agricultural activities around the park center on mixed cereal farming; however, cattle, and sheep on a much more limited basis, are raised. Twenty-two reports of predation on livestock were investigated during the period from 1975 to 1986 (Carbyn 1980, Paquet pers.comm.); investigation confirmed that seven domestic cattle had been preyed upon by wolves. In the summer of 1975 (prior to intensive field work), the loss of about 20 sheep was attributed to a single wolf, but this could not be confirmed (E. Coulson pers.com).

Wolf/livestock problems in the areas surrounding Riding Mountain National Park have not been widespread or serious. Livestock losses are most common in areas where fields and forest are interspersed as a mosaic.

Management Implications

Before the Riding Mountain National Park system is examined more closely, it is worthwhile to look at various management options in non-park areas. These options would vary between regions, depending on land use priorities and human demands. In any area where wolves still exist, one of the following three scenarios may occur that is relevant to the man/wolf/ungulate relationship (Figure 6):

(a) man is the dominant and only predator
(b) the wolf is the dominant and only predator, or shares the niche with one or more other large predators; or
(c) man and wolves are both predators, either of which can be dominant, depending on the situation.

Consequently, the purpose of wildlife management techniques can be:

(1) to eliminate man's influence, that is, to exclude all human hunting and giving free rein to natural processes;
(2) to eliminate all wolves and other large predators from an area, thereby managing game (non-carnivorous) solely for hunters; or
(3) to reduce man's influence and manipulate the numbers of predators (manipulation can take the form of eliminating all the members of some packs, leaving other packs intact or reducing numbers in all packs).

Options 1 and 2 are referred to as the "black" and "white" models, while option 3 is deemed the "grey" model. In the Riding Mountain National Park Man and Biosphere Reserve, options 1 and 2 are combined. In the 3000 km^2 core, option 1 is practiced; in the 6700 km^2 periphery, option 2 is practiced.

The predator/prey system in and around Riding Mountain National Park demonstrates how different land use practices can be combined to produce a "holistic" conservation strategy. I would define a holistic approach to conservation in much the same way that Aldo Leopold defined a

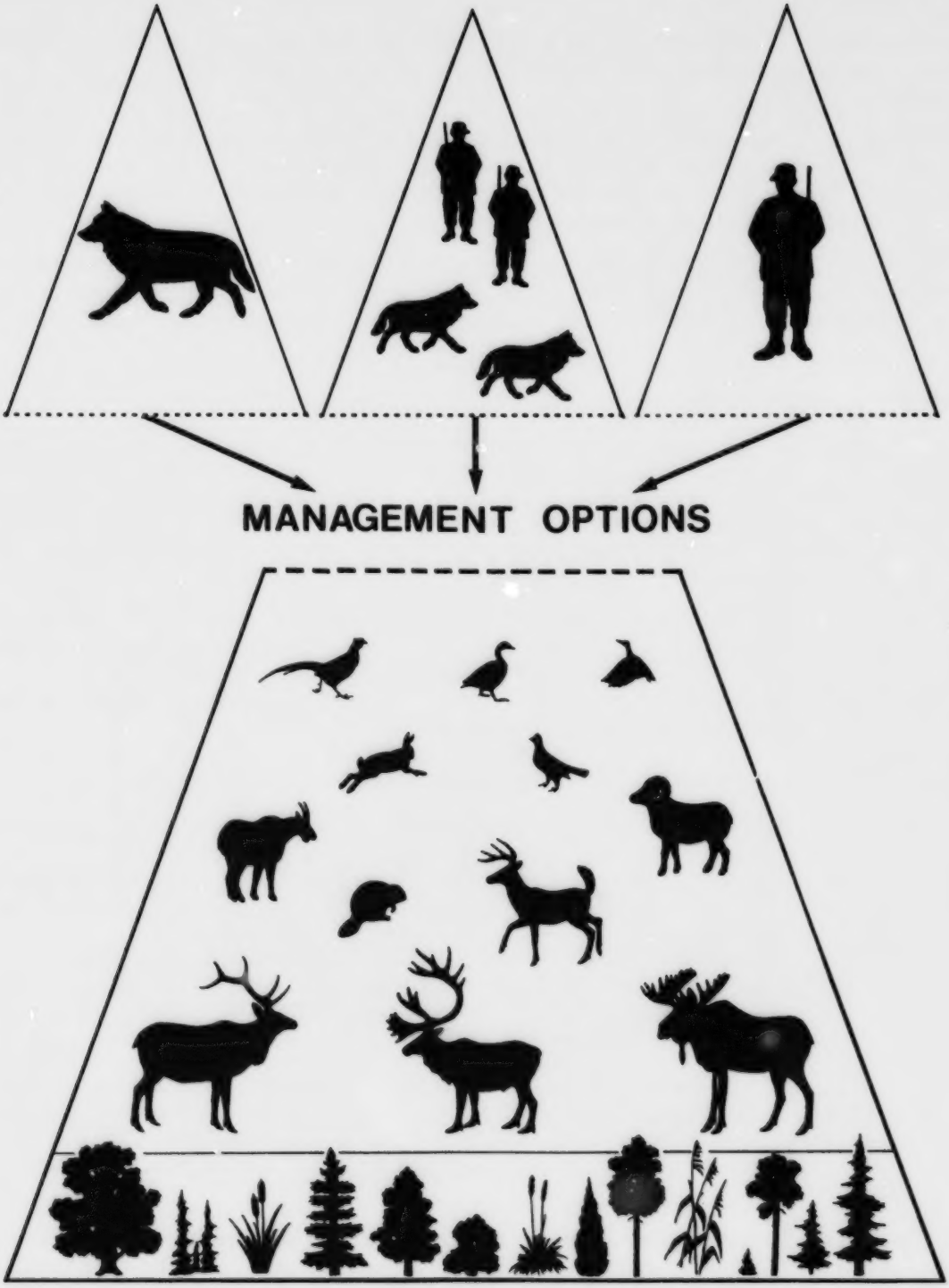

Figure 6. Wolves and man often compete for a common prey base. Wildlife management options range from complete predator protection to complete elimination.

land ethic. It is a relationship with the land in which "man, the prudent predator (hunter)" has a place to hunt (Leopold 1949), as much as "man, the preservationist" protects carnivores for their intrinsic value (Pimlott 1961).

The study of Riding Mountain National Park has taught me some important lessons. The management regimes for this ecosystem protect wolves and their prey, while the movement of elk, moose, and deer out of the park allows man to hunt, thereby, both "predators" are given the chance to exist side by side without destroying the system. Regardless of any ethical considerations of how man should relate to animals, the fact that humans are a part of nature cannot be ignored, and the realities that include man as part of the global ecology must be dealt with. I am personally very disturbed by the modern sociocultural trend in which, on the one hand, we destroy and pollute our planet to the point of threatening the very existence of all life on earth, while, on the other hand, we cling to the concept of the sanctity of life (anti-hunting philosophy) which removes us even further from the realities of the natural world.

Riding Mountain National Park is a good example of how man can influence an area, both in positive and negative ways. The park survived because man set it aside. Its wolves disappeared because of man's actions, and reappeared and survived again because of man's actions. Grizzlies are no longer a part of the Riding Mountain system, yet we rejoice in having the "wolf wilderness", even though it is without this co-predator. Since man, the hunter, obtains his prey when it leaves the park, Riding Mountain National Park serves a spectrum of societal needs - the complete protection of nature on the one hand, and the production of game for hunting on the other. There are, of course, many unknowns involved in deciding the best course of action for the future. For example, how is wolf behaviour affected by the loss of individuals, such as older pack members, when they are killed by man outside of the park? The territorial shifts observed between years may indicate that steady disruption of the packs is occurring. Are genes from neighbouring farm dogs gradually gaining a foothold in the wolf population? Are canid diseases, particularly the newly-evolved parvo-virus, having long-term effects? We cannot be sure that what exists in the park today will still be there tomorrow. A better understanding of the basic ecological processes involved becomes increasingly important in dealing with the changing situations.

Applicability of the Riding Mountain National Park model to other areas

The diversity of the ecosystem in Riding Mountain National Park - the soil conditions, plant diversity, and habitat interspersions - probably accounts for the high productivity of this region. Figuratively speaking, the park is like "Noah's Ark on the prairies"; it is an ark in a "sea of agricultural land". In this situation, wolves probably learn quickly not to abandon the ark, because if they do they may be killed by humans. The human predator will kill his competitor. Therefore, there is an incentive and a positive reinforcement for wolves to remain in the park.

No two areas are exactly alike - the knowledge gained from the study of this area cannot necessarily be applied directly to other situations. Nevertheless, there may be ways in which this park can be used as a model when other situations are studied. If wolves in protected zones are not geographically isolated from those in surrounding non-reserve status areas, an established buffer zone (i.e., a gradation from a strict nature reserve with no predator control to areas with partial predator control) may be necessary. The result could be the same as that achieved in the Riding Mountain National Park complex, where shared resources in protected areas benefit the preservation of resources in core areas, while human hunting occurs in adjacent areas.

What about the size of core areas? Within roughly a 3000 km^2 area, the wolf population in Riding Mountain National Park appears to be relatively secure in the short term. We know, from research in many parts of North America, that prey diversity, productivity, biomass, and availability dictate predator densities. Using radio-telemetry, it was determined that in Riding Mountain National Park the average wolf territory size is about 260 km^2. Does this mean that core sanctuaries of 6000 km^2 would be needed if the average size of wolf pack territories was 500 km^2? This may be the case, but there are many complicating factors, such as winter conditions, prey diversity, prey distribution, buffer prey species, migration routes of prey, escape terrain, and prey vulnerability, to name but a few of the variables. My own experience in two very different parks has taught me that the 3000 km^2 Riding Mountain National Park system is a better sanctuary for wolves than the 10752 km^2 mountainous terrain of Jasper National Park.

The lack of major wolf/livestock problems does not conform with the image of wolves as "blood thirsty" cattle killers. The wolves of Riding Mountain National Park quickly learn to fear man whenever they are shot at, illegally trapped, poisoned, or snared after they leave the confines of the park. Furthermore, with abundant prey in the park, there is good reason for wolves to remain there. It is conceivable that any major decline in the numbers or availability of prey could result in an increased incidence of predation on livestock.

Conclusion

The task of according this predator its rightful place in our modern world is difficult and challenging. Although it is fair to say that the old image of the wolf as a "beast of waste and desolation" has changed in the last 30 years, we cannot deny the fact that wolf predation can have an important impact on wild ungulate populations. Research in many North American settings has shown that this is the case, and that competition between man and carnivores is significant. This is particularly true when density and diversity of prey are low. In other areas, differences in prey diversity and density may require the use of different management schemes. Until now, Riding Mountain National Park has been an excellent example of the feasibility of a holistic approach to the conservation of nature. Man is preserving and using wildlife in a way that assures, for the short term

at least, the preservation of wolves, wilderness, and the wolves' prey, while at the same time, the human hunter is accorded a rightful place in the scheme of things. Such an approach to conservation, I believe, stands a better chance of success over time, than do more restricted approaches. The greater and more diversified that human interests are in renewable resources, the better our chances will be of preserving the environment for future generations. For wolves, this can best be achieved if the predator can exist in natural areas of our modern world, free from the human-placed constraints of ethnocentric value systems - yet conservation should not end there. To say that mankind should not be an integral part of natural systems places humanity in a very artifical position - one that, if it persists, will ultimately result in the destruction of our planet. In my opinion, the simplistic views of extremists on either side of the "wolf issue" demonstrate a lack of depth in their perception of the role of man in nature. It is in the role of responsible "stewards" that humans will ultimately achieve the kind of relationship with nature that Aldo Leopold so eloquently espoused 40 years ago, when he described his views of an appropriate "land ethic". Riding Mountain National Park is a good example of what can be achieved in a balanced conservation program. For the time being, wolves, man, and ungulates interact in a way that allows both the preservation and the wise use of the important elements in the ecosystem.

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Figure 1. Aerial view of Riding Mountain National Park (lower right), which is separated from Duck Mountain Provincial Park by approximately 35 km^2. Both parks have become isolated forest reserves, surrounded by agricultural areas.

Figure 2. Riding Mountain National Park, Man and Biosphere Reserve was established in 1986 and includes the park (core zone - 2978 km^2) and 18 municipalities (zone of cooperation - 6700 km^2).

Figure 3. Diagrammatic representation of wildlife abundance trends in Riding Mountain National Park from 1880 to 1980.

Figure 4. In the past, wolves competed with man for resources; this still occurs in some areas. Only in recent decades have wolves gained a more positive relationship with man.

Figure 5. Elk, moose, and wolf population trends, as obtained from annual park surveys carried out from 1975 to 1987 by Park wardens and Canadian Wildlife Service personnel.

Figure 6. Wolves and man often compete for a common prey base. Wildlife management options range from complete protection of the predator to complete elimination of the predator.

WOLVES AND UNGULATES IN BRITISH COLUMBIA'S NORTHEAST

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ABSTRACT: The relationship between wolves and four ungulate species (moose, mountain sheep, caribou, elk) is examined for British Columbia.

Early records indicate wolves were abundant in the 1940's then declined rapidly in the fifties as the province initiated an extensive wolf poisoning program. With the cessation of poisoning, wolf numbers increased rapidly. Wolf surveys and removal trials began in 1978. Over the last 10 years an average 100 wolves per year were removed from an average of 8000 km^2 area (6% of the northeast). During this 10-year period, overall wolf numbers increased in the northeast from about 1000 to 3500 wolves. Indications are that high pup mortality is now depressing the population growth in ungulate-depleted areas.

Where wolves were unmanaged, moose declined by about 8% per year. When wolf numbers were managed, moose juvenile proportions increased many fold and the population increased by about 8% per year. Decline of moose where wolves are unmanaged was found for one extensive zone to bottom at 0.08 moose per km^2.

Mountain sheep declined steadily in numbers (approximately 5-10% per year over 9 years) while wolves were unmanaged. When wolf numbers were managed juvenile proportions jumped and the populations increased.

Caribou declined substantially in the 1970's (11-12% with little hunting, 16% with heavy hunting) while wolves were unmanaged. Where wolves were managed juvenile survival improved and numbers increased at 6% per year.

The majority of the elk in the northeast declined at an average of 5% per year in the first half of the 1980's. When wolves were managed juvenile survival increased many fold but program continuity was insufficient to measure a population increase.

Ungulate numbers in the northeast are concluded to be limited by wolf numbers. The multiple species prey base and the ability of wolves to change kill rate over a large range depending on prey density result in the natural balance stabilizing at low prey densities and moderate wolf numbers.

Management of wolf numbers would, over the long term, allow the same number of wolves but many more ungulates.

INTRODUCTION

Ungulates were felt to be declining in British Columbia's northeast in the 1970's (local reports; Bergerud 1978). In consequence, investigations were begun in 1978 to identify population trends for four ungulate species - moose (*Alces alces*), thinhorn sheep (*Ovis dalli stonei*), caribou (*Rangifer tarandus*) and elk (*Cervus elaphus*), to identify their recruitment and to identify wolf numbers. Subsequently wolf numbers were reduced in two areas to elucidate the wolf - ungulate interaction.

British Columbia's northeast (Figure 1) is a diverse area of some 125 000 km^2 typified by low winter snowfall yet substantial summer rainfall (Figure 2, B.C. Department of Agriculture 1971). Physiographically, the entire region is in the Arctic watershed. The vegetation (following Krajina 1965, 1972) is primarily described as Boreal White and Black Spruce, Spruce-Willow-Birch and Alpine Tundra Biogeoclimatic Zones (Farley 1977). A striking feature, however, is the considerable role of fire in altering vegetation composition.

The northeast has a rich diversity of ungulates approximately estimated (Elliott 1988) at 25 000 moose, 6000 mountain sheep, 4000 elk, 2000 caribou, 2000 mountain goat (*Oreamnos americanus*), 1000 deer (*Odocoileus hemionus* and *O. virginianus*), and 400 bison (*Bison bison*). Beaver (*Castor canadensis*) are also present. Large predators include about 3000 wolves (Elliott 1988), 4000 black bear (*Ursus americanus*) and 2000 grizzly bear (*Ursus arctos*).

ANIMAL NUMBERS

WOLF

Actual count data for wolves are nonexistent for the northeast (or elsewhere in the province) prior to 1978. A number of indicators, however, suggest a pattern for the last 50 years.

Wolf bounties were paid in British Columbia until 1956. Figure 3 shows the trend in number of wolves bountied for the last three decades. It can be seen that numbers were moderate in the 1930's, high in the 1940's, then declined rapidly as the province initiated an extensive wolf poisoning program in the 1950's.

Wolf trapping records for the province have been available since 1962 (Figure 3). These suggest low wolf numbers from 1963 to 1968 (depending upon area) while wolf poisoning continued. Once wolf poisoning was stopped, wolf numbers rapidly increased for the 1970's and 1980's.

A survey of longtime northern British Columbia outfitters was conducted by Bergerud (1978). It suggests (Figure 3) a trend similar to that shown by the bounty and trapping statistics.

A summary of all wolf surveys each year in the northeast or immediately adjacent region is given in Figure 4. An annual average of 15 300 km^2 (6500 - 30 900 km^2) were enumerated 8 of the last 9 years for wolves in areas unmanaged for wolf numbers. The areas counted were not constant each year; however, the data suggest an increase from about 7 wolves per 1000 km^2 to 27 wolves per 1000 km^2 in 1986. This converts to an increase from about 1000 wolves to 3500 wolves in the northeast over that period. Bergerud (1978) suggests that the wolf numbers in portions of the northeast in the mid to late 1970's may have been lowered by illegal killing. It may be that with increased Wildlife Branch presence as a result of the wolf management program, illegal killing declined allowing a general increase in wolf numbers (other than temporary declines in the small areas managed for wolf numbers by the Wildlife Branch).

Table 1 summarizes the wolf removals in the northeast. From 1978 to 1987, an average of 100 wolves per year were removed from an 8000 km^2 area. Removal levels from the northeast as a whole have always been well below the conservative 30% considered minimum to have any effect upon overall wolf

numbers (Keith 1983). This, of course, also follows from the large increase in wolf numbers that occurred simultaneously (Figure 4).

The 4-year period (1982-85) of annual reduction of wolf numbers in the Kechika enabled us to look for trends in various demographic feature of an exploited wolf population (Figure 5). Sex ratio showed no strong trend, averaging 43% females. Proportions of juveniles, however, declined steadily over this period from 37% juveniles pre-reduction to 19% juveniles after 3 years of reduction. Since numbers of wolves increased about three-fold each year in the 12 months following reduction, it is apparent that reproduction by the remaining wolves would account for little of the increase. The increase comes from surplus wolves in surrounding areas immigrating to these areas. The declining recruitment would thus be a measure of what was happening to the wolf population as a whole. Keith (1983) found that a declining ungulate base and increasing number of wolves lead to reduced wolf recruitment.

Coat colour (Figure 5) shifted during the reduction period from 19% blacks pre-reduction to an average 54% post-reduction. Work with birds (O'Donald 1977) has shown that increased melanism within a species is associated with more aggressive (and thus appropriate to colonizing) behaviour.

Table 1. Wolf reductions in the northeast

Year	Location	Area (km^2)	No. Removed
1978	Kechika	3000	22
1979	Kechika	3000	25
1980	Kechika	3000	23
1982	Kechika	4000	70
1983	Kechika	7000	89
1984	Kechika	10000	105
1984	Muskwa	7000	182
1985	Kechika	18000	157
1985	Muskwa	14000	198
1987	Muskwa	10000	125

MOOSE

Areas where absolute moose density estimation has occurred are shown on Figure 6. The land area involved, date of the survey and moose estimate are given in Table 2. Moose densities have not remained static, however. Three areas where wolves have not been managed have density estimates from two different times (Figure 7). As shown in Table 2, the Pink area was surveyed in 1979 and found to contain 1.7±0.25 moose/km^2. When 1315 km^2 of this area was surveyed in 1984, that density had dropped to 1.1±0.01 moose/km^2 (.10>p>.05). Likewise, the Core area was surveyed in 1982 and found to contain 1.0±0.3 moose/km^2. When this area was resurveyed in 1985, the density was then 0.8±0.16 moose/km^2 (.5>p>.2). Finally, the eastern 1000 km^2 of the Goulet area was found by Goulet and Haddow (1985) to contain 0.60±0.88 moose/km^2 in 1981. The Liard survey of 900 km^2 of the same area in 1986 found only 0.09±0.03 km^2 (p>.5). Although none of these three rates were statistically significant by themselves, together there was a consistent trend of decline.

Sumanik and Demarchi (1977a,b) undertook an extensive series of transect surveys. Their survey results present abundance classes of moose seen per hour (Figure 8). Their classification system recognized six levels: 90 or more moose per hour seen (A), 60-89 (B), 45-59 (C), 30-44 (D), 1-29 (E) and 0 (F).

Table 2. Absolute density moose counts

Site[a]	Area (km^2)	Date of Survey	Moose/km^2
Lincoln[b]	2600	02/79	0.5
Horseranch	1500	02/79	0.3
Pink	900	02/79	1.7
Goulet[c]	6700	02/81	0.6
Core	1400	02/82	1.0
Middle Creek	400	02/84	0.7
Tierney	400	02/85	1.7
Liard	900	02/86	0.09
Fort Nelson	25000	01/88	0.08

[a] See figure
[b] From Lincoln 1979
[c] From Goulet and Haddow 1985

Figure 9 presents the results of a 1986 survey utilizing similar methodology and classification systems. For the 2300 km covered by both surveys, it can be calculated that Sumanik and Demarchi report 57 moose per hour seen whereas the 1986 survey saw only 24 per hour. Four surveys over a 6-week period of the same 150 km segment in 1986 showed no great variation in sightings (23.4±1.2 moose/hour), although snow conditions varied little over this period. In 1967, the snow was somewhat deeper though rather fluffier than in 1986 while the snowpack in 1968, 1969 and 1970 was much like the snowpack in 1986 (February 1 comparisons, Province of British Columbia snow measurement records for Fort Nelson). The role of snowpack in effecting dispersion in the northeast is poorly known; however, the variations between survey periods appear modest. Given approximately similar survey snowpacks, moderate precision of the technique, a better viewing platform for the 1986 surveys and yet a drop from a mean of 57 to 24 moose per hour seen (late 1960's versus 1986); the strip surveys suggest a decline in moose numbers.

The 4 years of annual reduction of wolf numbers in the Kechika (Table 1) allow an examination of the relationship between wolf numbers and juvenile moose survival. Figure 10 presents those data. Where wolf numbers were unaltered, the recruitment was consistently low. For the wolf-managed Kechika, recruitment was initially low, increased many fold when wolves were reduced (ten fold for the third and fourth years of removal compared to the control) and then substantially declined when removal was stopped (and wolf populations rebuilt). The Middle Creek moose census area (Figure 6) is located in the wolf-managed Kechika. That area had an estimated 0.69 (±0.13) moose/km^2 (Figure 7). This trend to increase is in sharp contrast to the trend where wolves were unmanaged. Van Ballenberghe and Dart (1982) suggest a maximum possible rate of moose population increase of 14% per year derived for an Alaskan moose population. The estimates found for Middle Creek (with wolf numbers recovering for the last 2 years) indicate a rate of increase of 8% per year.

MOUNTAIN SHEEP

Four years of annual wolf reduction in the Kechika (Table 1) provide insight into the role of the wolf in juvenile mountain sheep survival. Figure 11 presents the juvenile proportions with wolves managed and unmanaged. While wolf numbers were low, more than twice the number of lambs (per adult ewe) survived to 21 months. After wolf management ceased, juvenile survival declined to levels found elsewhere where wolves were unmanaged.

Juvenile mountain sheep survival was reflected by trends in adult numbers. Figure 12 shows 10 areas that were censused in several years for adult mountain sheep. These surveys represented minimum counts. One area of 100 km^2 was counted five times in 1983, with a range of 102 to 126 sheep. Although the true number of sheep cannot be determined, it does suggest the methodology is sufficiently consistent to detect major population trends. Figure 13 indicates the results of these counts. Prior to the influx of new juveniles resulting from wolf management, all census areas showed a trend to decline. Thereafter, the trend was to increase beginning with Bridge, Rusty and Netson, which were the only areas with wolf management in 1982. Frog was added in 1983, then all areas but Major and Rapid, in 1984. All areas were wolf managed in 1985.

CARIBOU

Bergerud (1978) examined the status of caribou in the northeast and elsewhere in 1978. For six herds he also identified numbers present approximately 10 years previously (Figure 14). These herds were found to have declined at about 16% per year over that period on average. Hunting was, however, a factor with the heavily hunted herds declining more rapidly than those which were virtually unhunted.

The Horseranch Range caribou have gone through two periods of managed wolf numbers: 1978-80 and 1985. This is reflected in the trends in wolf numbers utilizing that herd's summer range (Figure 15). Caribou recruitments to October have, in turn, shown a close negative correlation with wolf numbers (Figure 15). Where wolf numbers were high, survival of caribou juveniles was low and vice versa with a seven-fold range (7 to 51 calves/100 cows).

Snowpack and hence, spring snow ablation plays a role in the predation process. In an early spring, there were more extensive snow-free areas for dispersion of cows for calving (caribou calve on snow-free areas so that the brown calves are camouflaged). The more dispersed the calving in space, the more search time required for a predator to find each calf. The influence of this aspect upon the wolf/caribou calf survival relationship can be seen in Figure 15.

For the period 1977-82, Bergerud and Elliott (1986) compared the Horseranch Range caribou herd to two other herds in northern British Columbia: the Spatsizi-Lawyers and Level-Kawdy. The Horseranch herd, with 3 years of reduced and 2 years of recovering wolf numbers, increased at an average of

6% per year during that period. The other two herds, with no management of wolf numbers, declined by an average of 11-12% per year.

ELK

The main elk herd in the Muskwa drainage of the northeast has been monitored for the period of 1982 through 1988. Wolf numbers in that area were reduced in 1984, 1985 and 1987 (Figure 16). Survival of elk calves and yearlings as measured by recruitment correlated closely with the area per wolf (Figure 16). The lowest managed density of wolves resulted in about five times the number of calves per cow as did the high density of wolves when they were unmanaged. Yearling proportions showed a four-fold range with wolf number changes.

The smaller herd of 100-200 elk in the Kechika was monitored from autumn 1985 to spring 1987 and showed a similar response to wolf density as the herd in the Muskwa (Figure 16).

The non-calf component of the Muskwa elk herd declined at an average rate of 5% per year from 1982 (3730 non-calf elk) to 1985 (3137 non-calf elk), a period of 2 years of unmanaged and 1 year of moderately reduced wolf numbers. There has been no extended period of wolf management to derive an elk population growth rate in the presence of low wolf numbers.

DISCUSSION

The evidence supports the hypothesis that, for the last decade, ungulate numbers (at least moose, mountain sheep, caribou and elk) have been limited in the northeast by wolf predation. Further, the limitation has been such that the populations of these ungulates have declined substantially. Simultaneous with these declines has been an apparent increase in wolf numbers. I believe this situation results from the earlier wildlife management in the area, the tremendous plasticity in the functional response of wolves to prey availability and the rich multiprey base of the wolf/ungulate complex.

The widespread poisoning of wolves in the 1950's and 1960's resulted in low wolf numbers for 15 to 20 years (Figure 3). Although not directly measured, hunting statistics and interviews of long time outdoor people (Bergerud and Elliott 1986) suggest that northern British Columbia, including the northeast, had a large increase in ungulates by the end of that period. At the cessation of poisoning there was, therefore, no external control on wolf numbers and a vast prey base available.

An examination of kill rates by wolves for six different prey densities (Table 3) shows that food consumption (Y = the consumable kg killed/kg wolf/day) increases as prey density (X = the prey density converted to moose biomass equivalents) increases:

$$Y = 0.2X$$

with r = .9332 (.01>p>.001). From this it follows that different ungulate prey/wolf ratios will, for the same density of wolves, have a constant prey mortality rate. This functional response is expected where search time is a lengthy component of the prey capture cycle (Elliott *et al.* 1977).

Table 3. Wolf consumable prey kill rates for different prey densities

Kill Rate[a]	Prey Density (/km^2)	Source
0.08	moose 0.17	Messier 1984
0.11	moose 0.37	Messier 1984
0.12	moose 0.80	Peterson *et al.* 1984
0.16 (0.13 - 0.19)	moose 1.20	Mech 1966
0.39	moose equiv. 1.70	Elliott 1987
0.42	moose equiv. 1.93	Carbyn 1983

[a] kg of consumable prey killed/kg of wolf/day, includes abandonment of consumable portions

Multiple prey confound the predator/prey interaction. One aspect of this results from the addition of different prey reducing the escape options of the prey group. Thus, for example, in a one prey, one predator situation, there may be a number of strategies, such as migration, use of cliffs or water, that allow considerable prey escape from predation at certain times of the year. The numerical response of the predator (that is, its numbers) would be expected to relate to the time of year when prey is least obtainable. The introduction of one or more other types of prey utilizing seasonal escape strategies, but at different times of the year not only provides more food overall, but more food at periods that were otherwise limiting. Multiple prey may result then in more wolves than the sum of what each prey alone could support. However, the preference by

wolves for certain species (based upon their ease of killing) results in those species receiving an impact beyond even the increase, resulting from the greater wolves supported by a multiple prey system. The consequence of this preference is the sequential decline of prey species. It appears that deer were the first to be selected by wolves in the northeast, being reduced to low levels soon after the buildup of wolves following the cessation of wolf control (local reports). Caribou were then preferred and reduced to low numbers in the early 1970's (Bergerud 1978). Mountain goat seemed to be the next preference, substantially declining in the 1970's (Elliott, unpubl.). This was followed by mountain sheep, which declined steadily in the latter half of the 1970's. Then, in the late 1970's and early 1980's, elk (Peck 1988) and moose populations began to collapse. An increase in bison mortality seems to be a final recent stage with yearling survival such that 13-month yearling proportions have now dropped to about 10% from over 30% around 1980 (Elliott, unpubl.). The timing, of course, has shown variation across the northeast depending upon local prey diversity. Bergerud and Elliott (1986) describe a variant of this where a new prey (moose) is introduced to a simple predator/prey (wolf/ungulate) system.

The declines of ungulates can be expected to level. Some populations of the preferred species have been exterminated or reduced to very low levels already (Halkett, Ram, Helicopter, Yakatchie, Pantreath and Buckinghorse mountain sheep, plus Trutch, Snake, Aline, Kechika (prior to reintroduction) and Smith elk), while others are still declining to unknown lows. However, a primary species such as the moose is unlikely to vanish totally. There is evidence to support this. The Fort Nelson moose count area (Figure 6), with its 0.08 moose/km^2, had 25 total male and female 9-month calves per 100 cows (1 year or older). This is close to what is needed to sustain the existing cow numbers: Peterson (1977) found an adult annual natural mortality rate for moose on Isle Royale of 13%, Gasaway *et al.* (1983) found 20% for Alaska, while Watts (unpubl.) found 15% for the British Columbia Peace River area. Wolves were not counted for the Fort Nelson unit; however, sign was commonly encountered during the moose survey. The recruitment status for those wolves is not directly known, but the declining recruitment of the immigrants to the reduction area (Figure 5) is indicative of declining status in the unmanaged wolf population. Certainly, 1985 recruitment levels were below those reported for most wolf populations (Keith 1983).

The correlation between the decline of wolves during the large scale poisoning program of the 1950's and 1960's, with the increase in the ungulate herds, then their decline as wolf numbers recovered following the cessation of poisoning, suggests a cause and effect has occurred over that 40-year time frame, similar

to that documented in this report, for the last 10 years. Two generalities seem forthcoming from this. First, ungulate species diversity and numbers will be low and wolf numbers moderate, if the predator/prey balance is not managed. There may be occasional eruptions of localized ungulate populations, but, these will be the exception (Bergerud and Elliott 1986). Second, pulse management of predator numbers can be expected to increase predator/prey fluctuations in the northeast. The reverse of these two, that is, the dampening of fluctuations, and maintenance at a high system diversity, would be the ecologically desirable state.

Extrapolating back in time from present estimates and measured population trends for known populations, suggests there were over 100 000 ungulates in the northeast in the early 1970's. We now have about one-third of that, and the ungulates in their remaining areas of relative abundance are still declining. Indeed, most areas now have insufficient ungulates to allow habitat protection against competing uses. Further, wolves are declining as the ungulates are depleted. The northeast's wildlife has and could again contribute substantially to British Columbia's native people's heritage, all people's social well-being, and even the province's economic well-being. Unavoidably, this latter feature is imperative, if there is to be long-term protection for the area's wildlife and necessary habitat. This will not happen with low ungulate and low to moderate wolf populations, however. With the management of wolf numbers, we could have moderate to high ungulate populations, and still have moderate wolf populations with a defendable land base for both.

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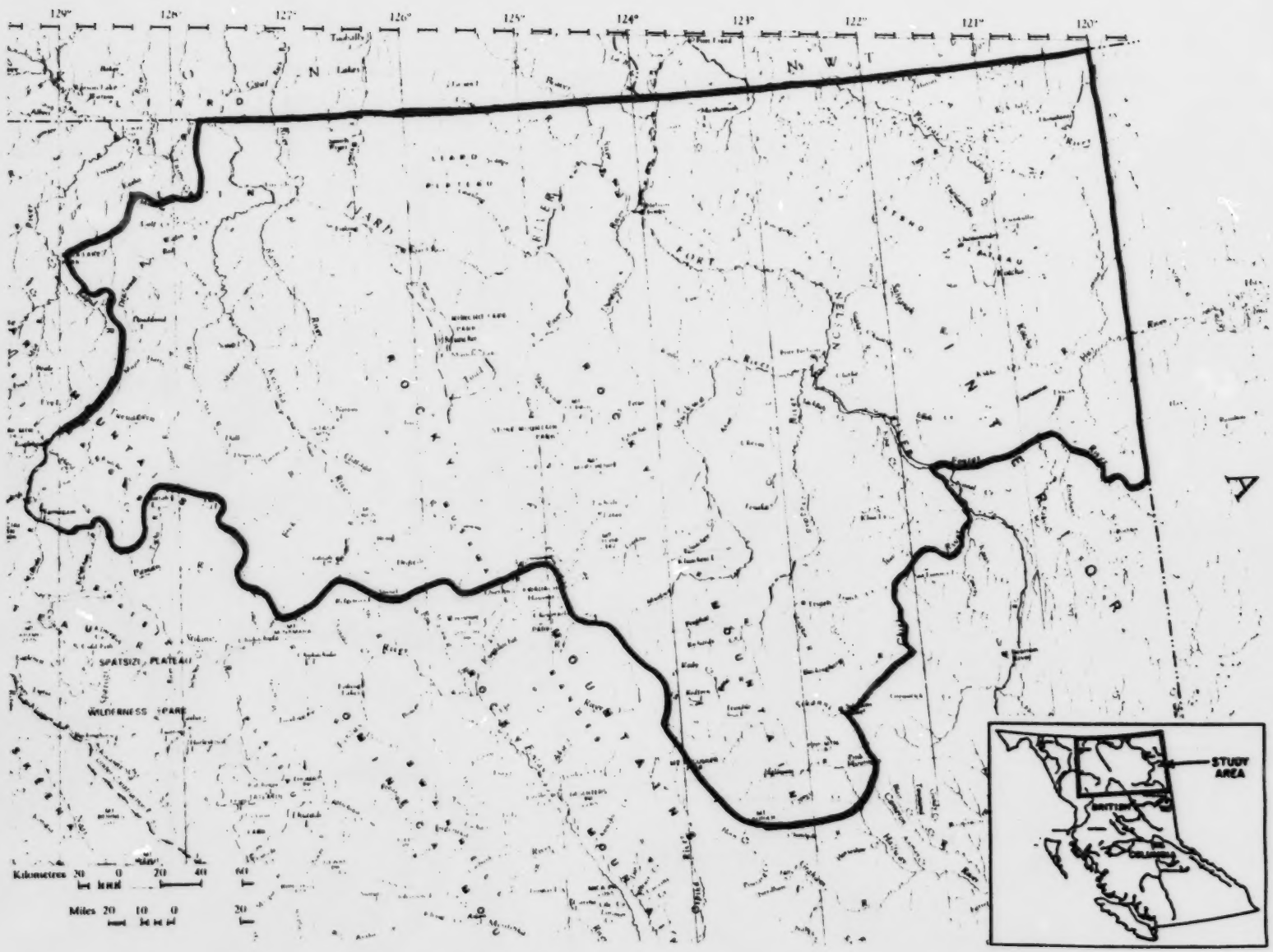


Figure 1. Northeast British Columbia.

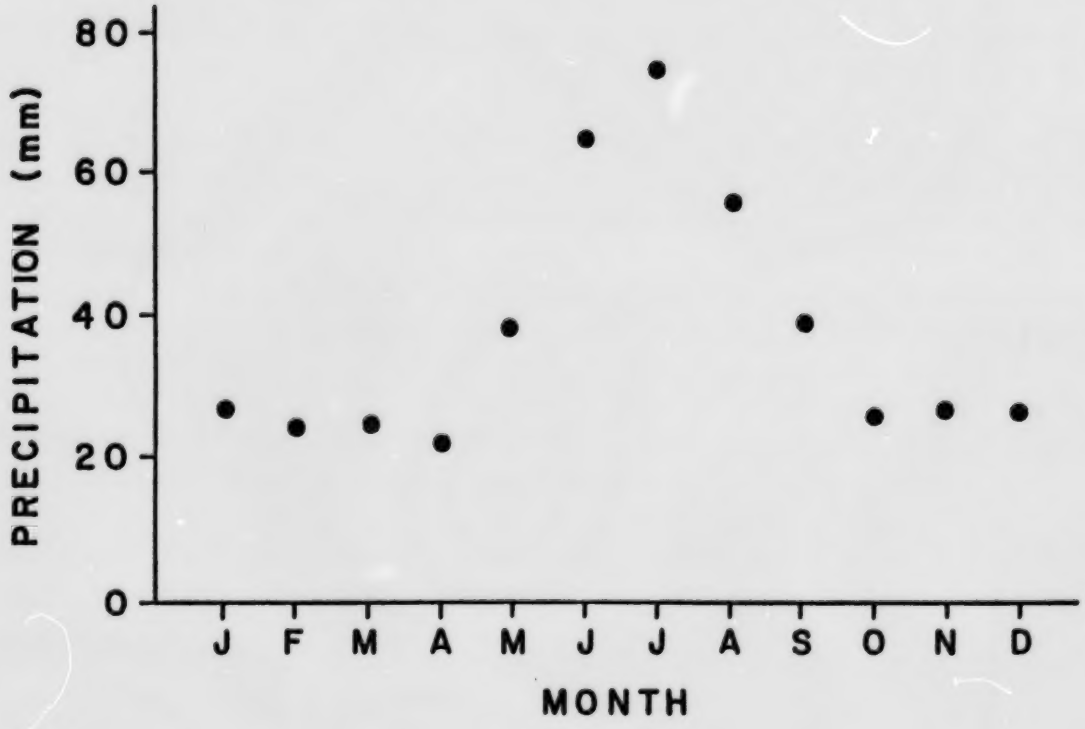
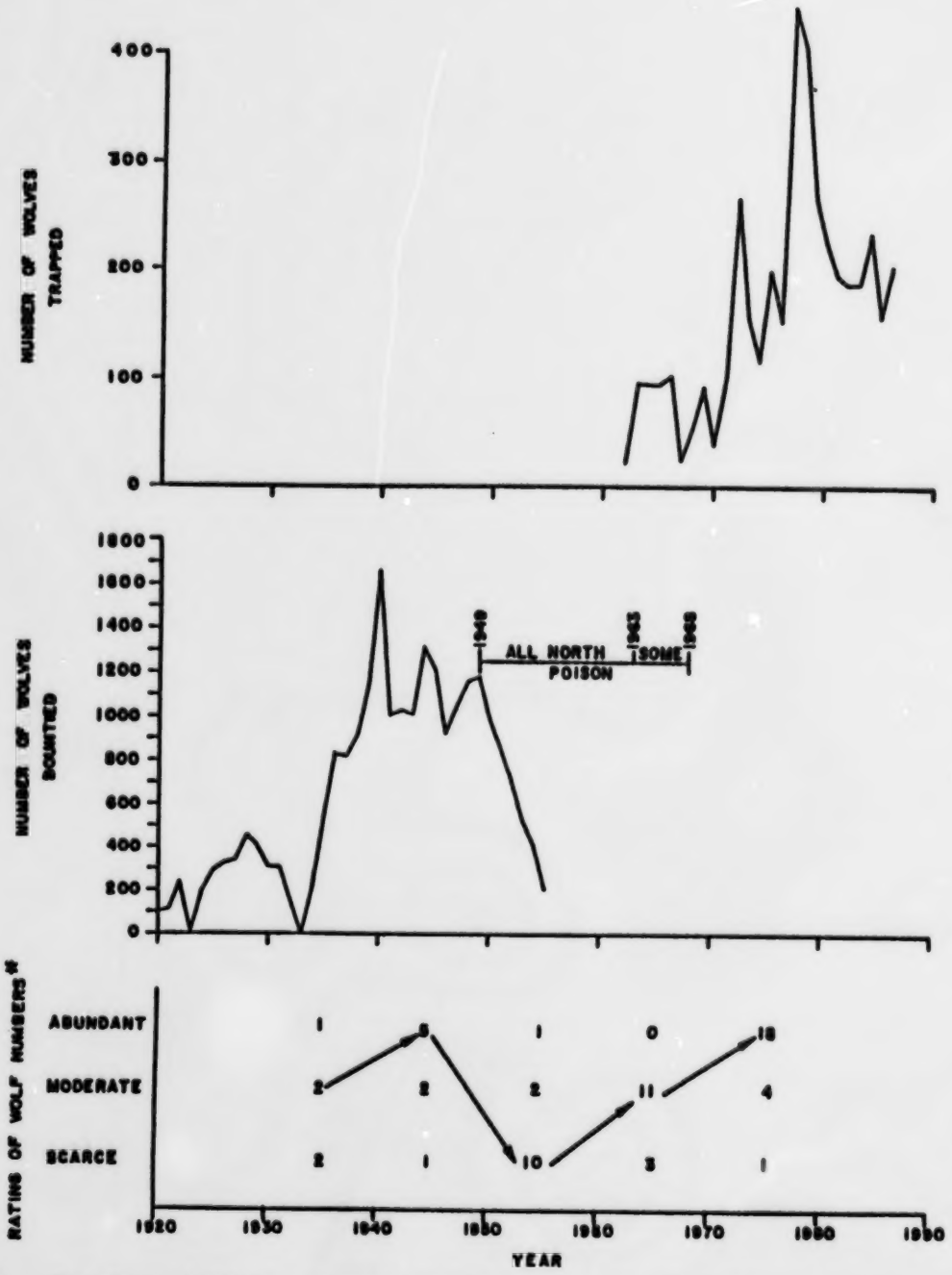


Figure 2. Thirty-year mean precipitation measured at Fort Nelson.



* From Bergerud 1978 (a questionnaire response by professional outfitters of long residence in northern British Columbia):

Abundant	-	fresh signs or animals seen most days
Moderate	-	tracks seen but no animals
Scarce	-	few or no tracks
	-	apparant population trend

Figure 3. Wolf trends in British Columbia.

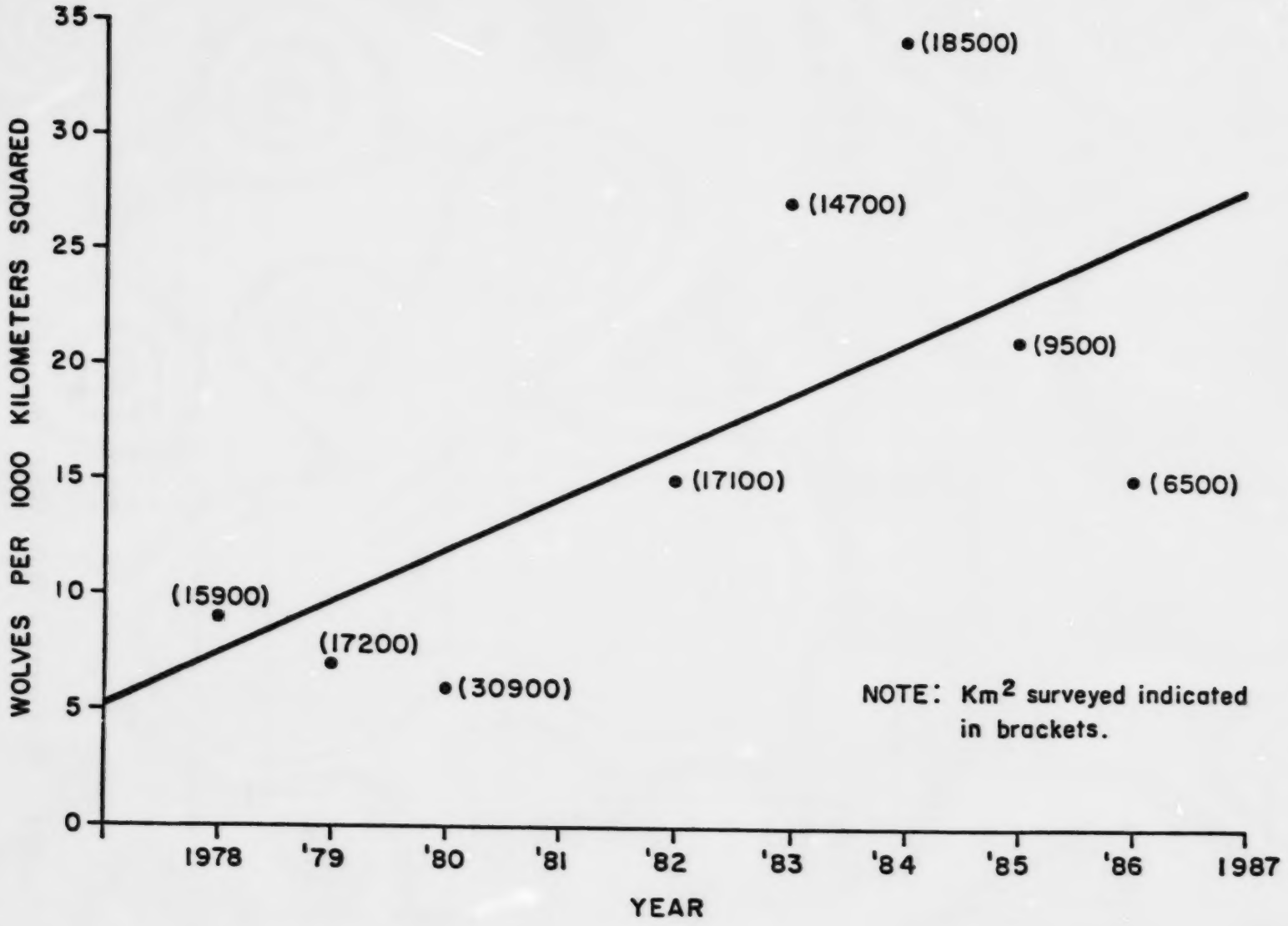


Figure 4. Wolf numbers in the Northeast.

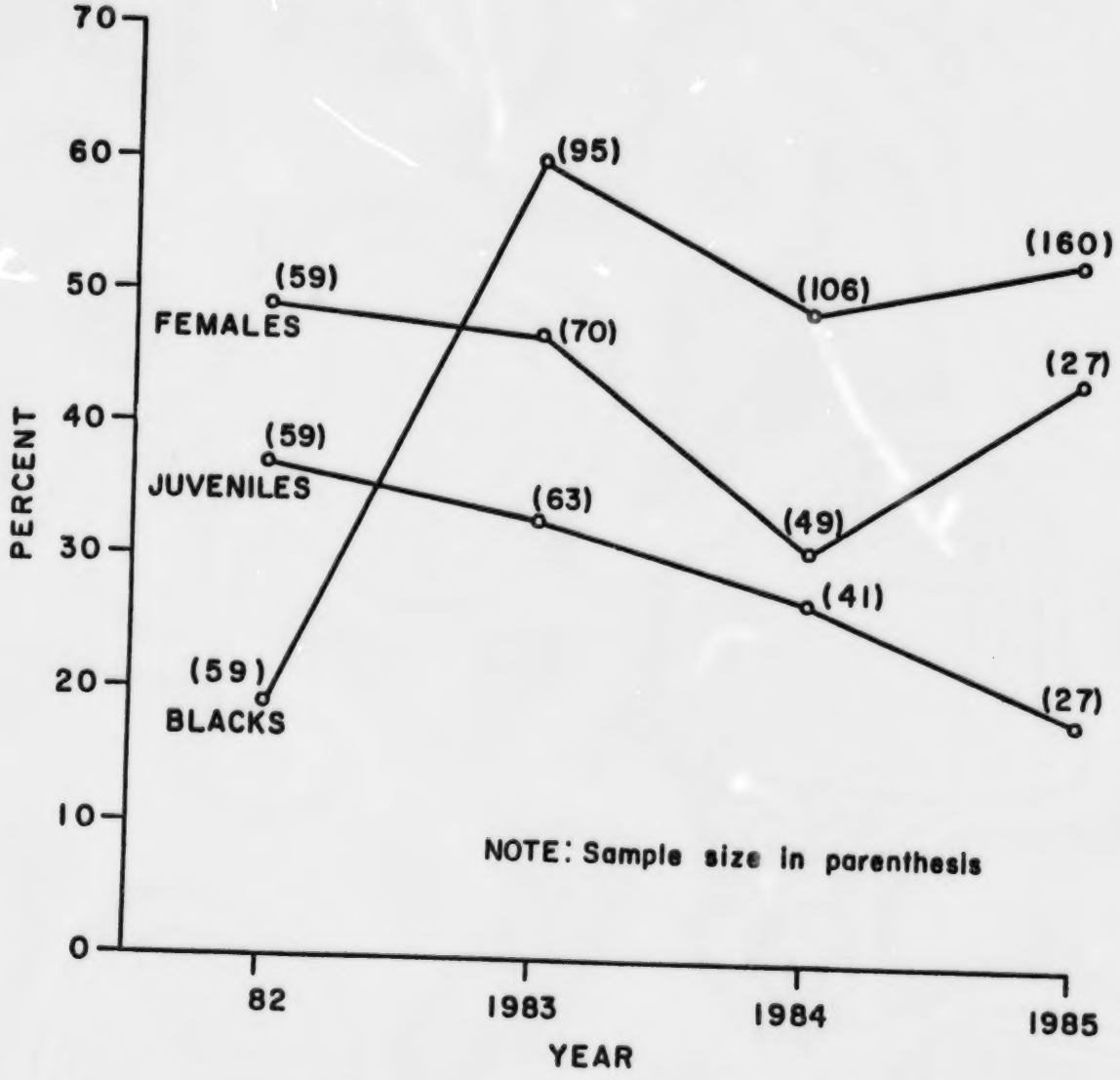


Figure 5. Demographic aspects of wolves in the 4-year Kechika removal area.

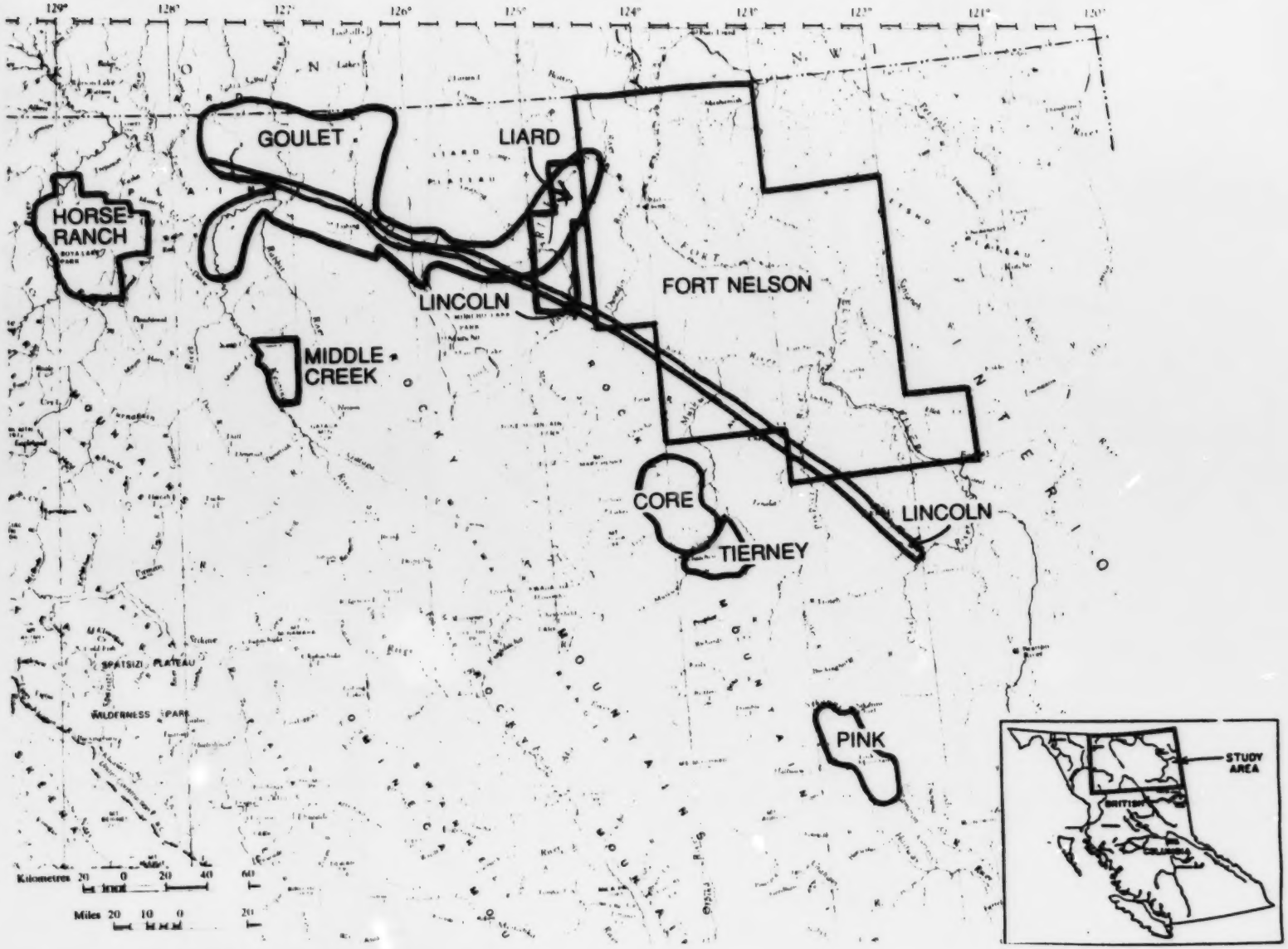


Figure 6. Moose absolute count areas.

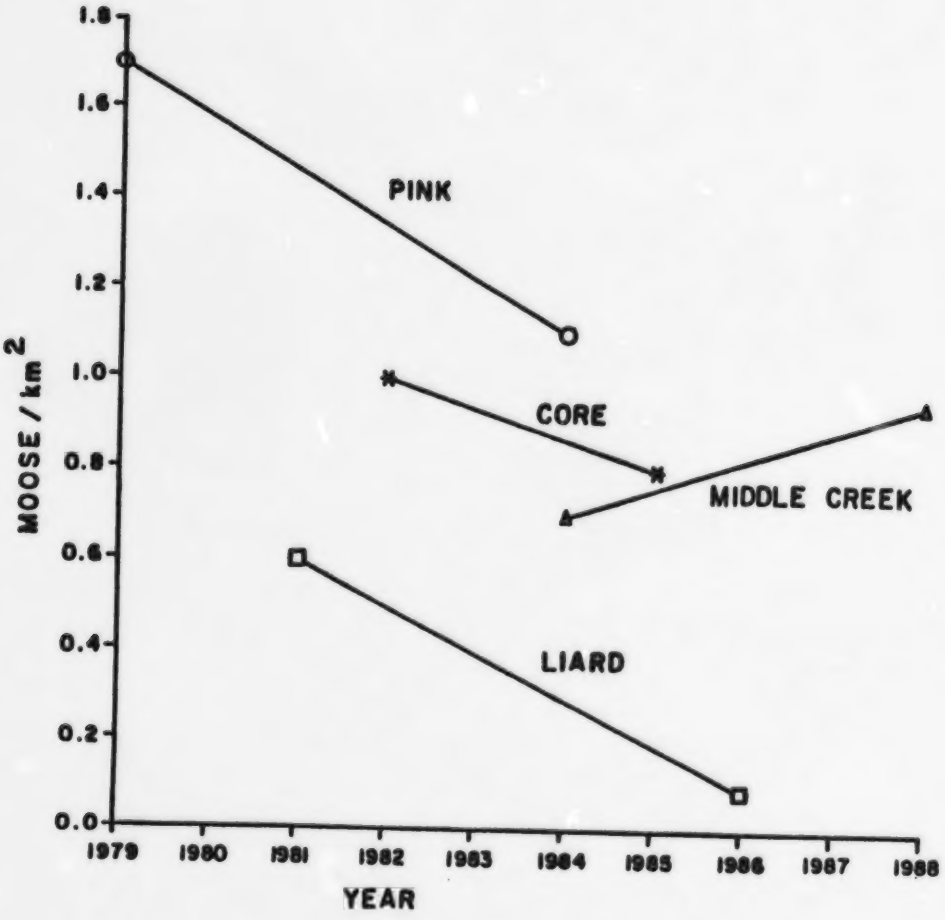


Figure 7. Temporal variation in moose densities in British Columbia's Northeast where wolves were unmanaged (Pink, Liard, and Core - except one year of moderate reduction for the Core area) and managed (Middle Creek).

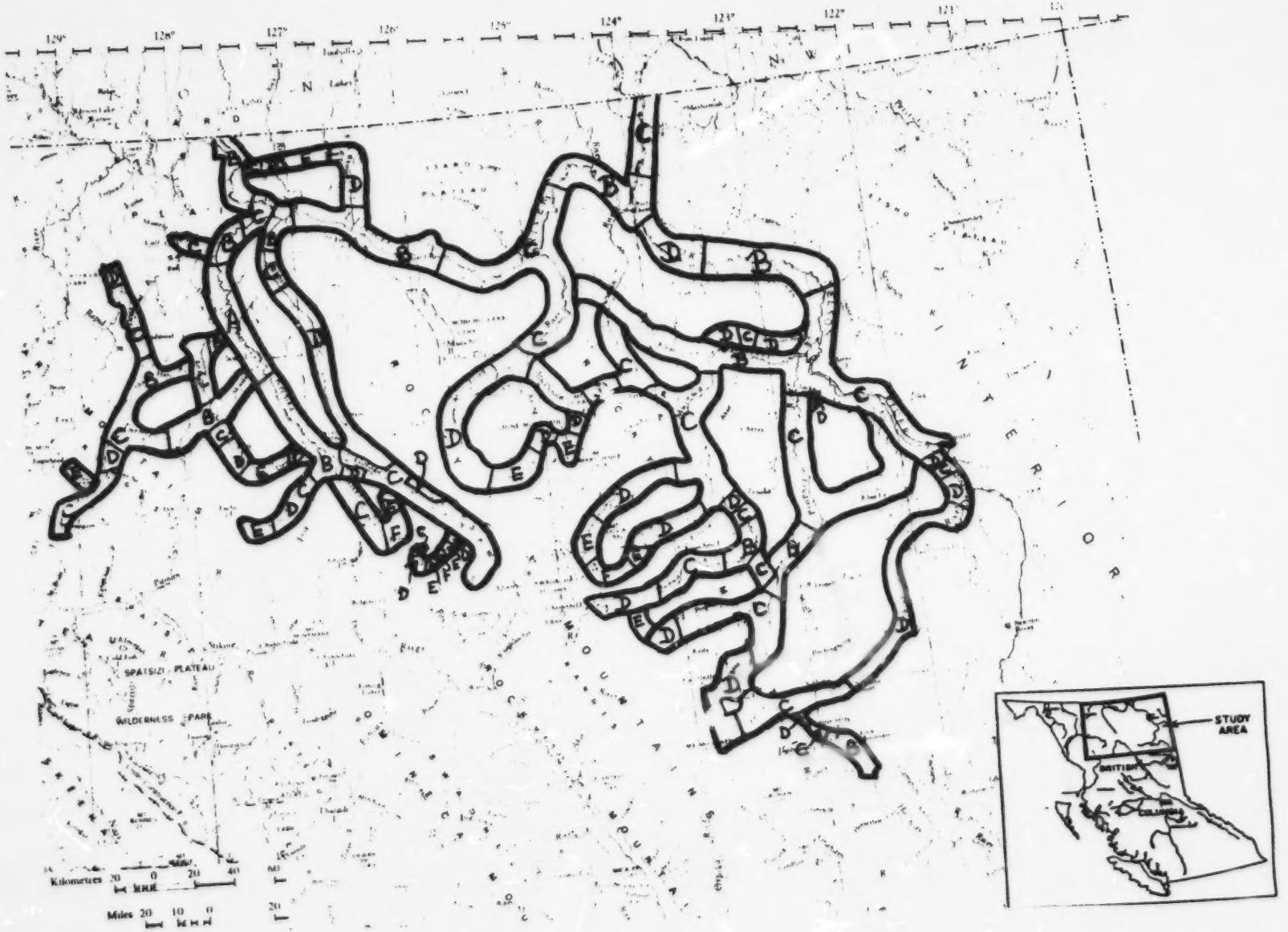


Figure 8. Moose abundance strips for northeast British Columbia, 1967 -

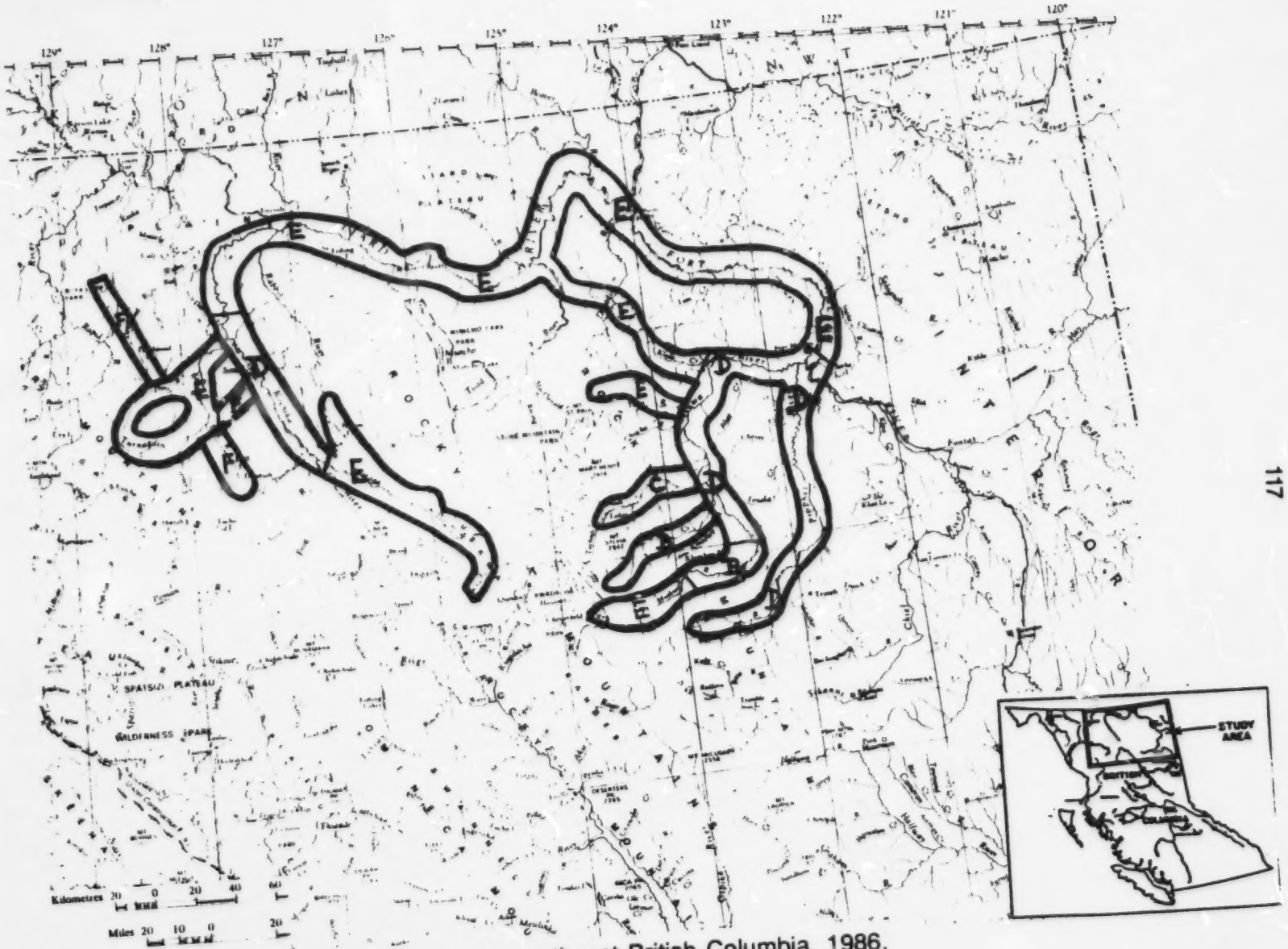


Figure 9. Moose abundance strips for northeast British Columbia, 1986.

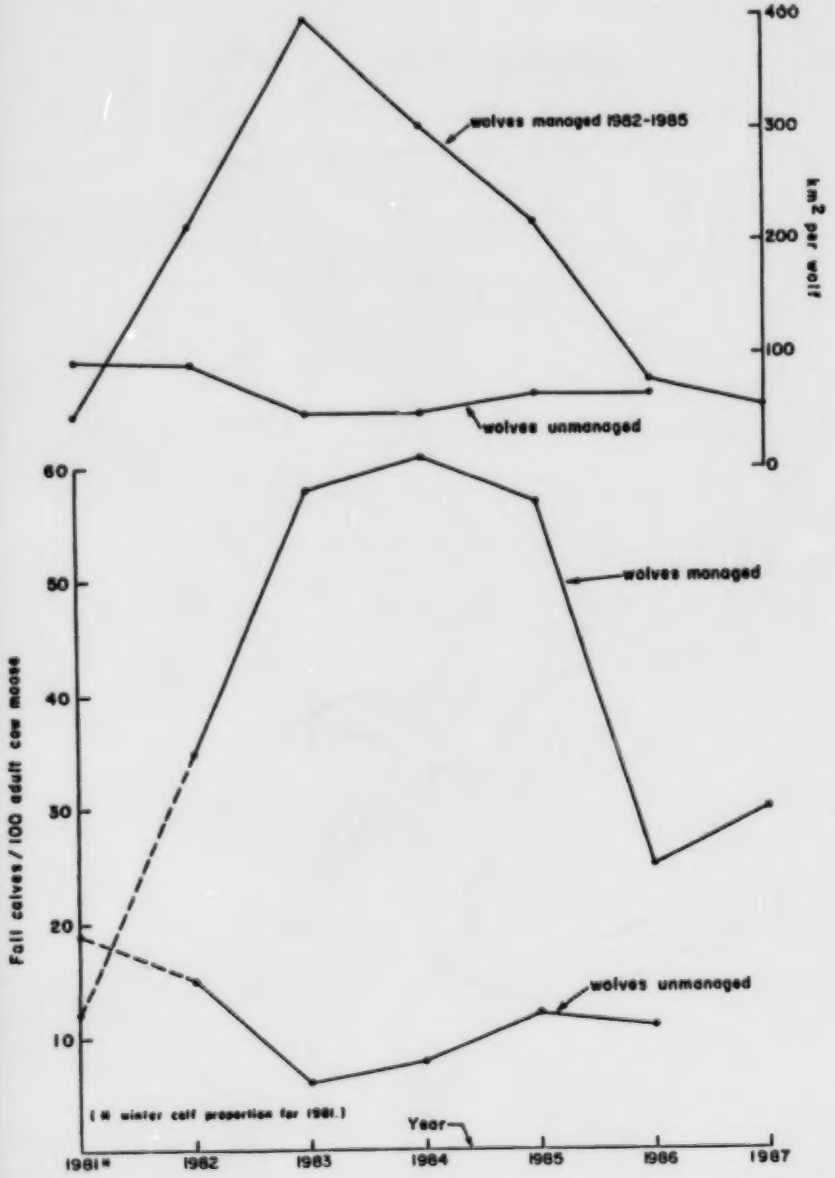


Figure 10. Area per wolf and juvenile survival in moose for wolf managed and unmanaged portions of the Kechika.

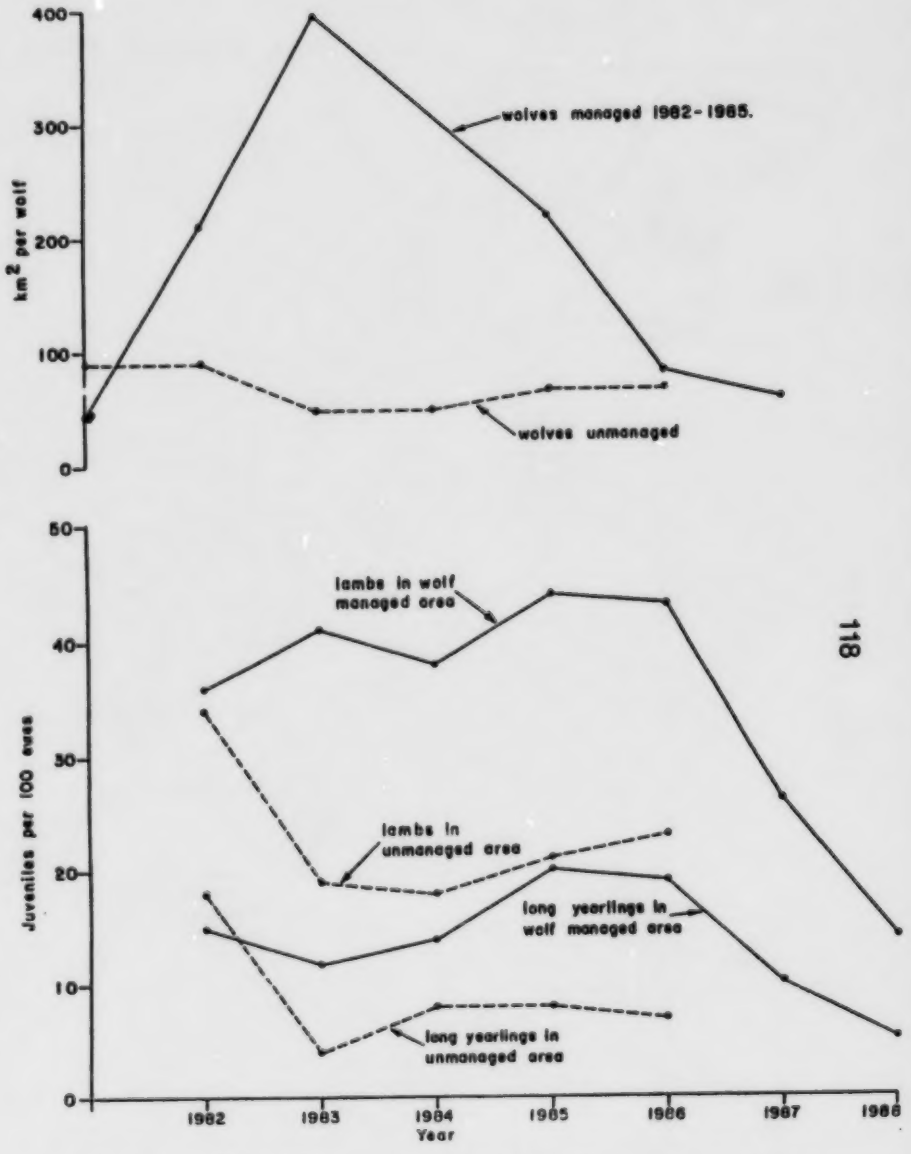


Figure 11. Area per wolf and juvenile survival in mountain sheep for wolf managed and unmanaged portions of the Kechika.

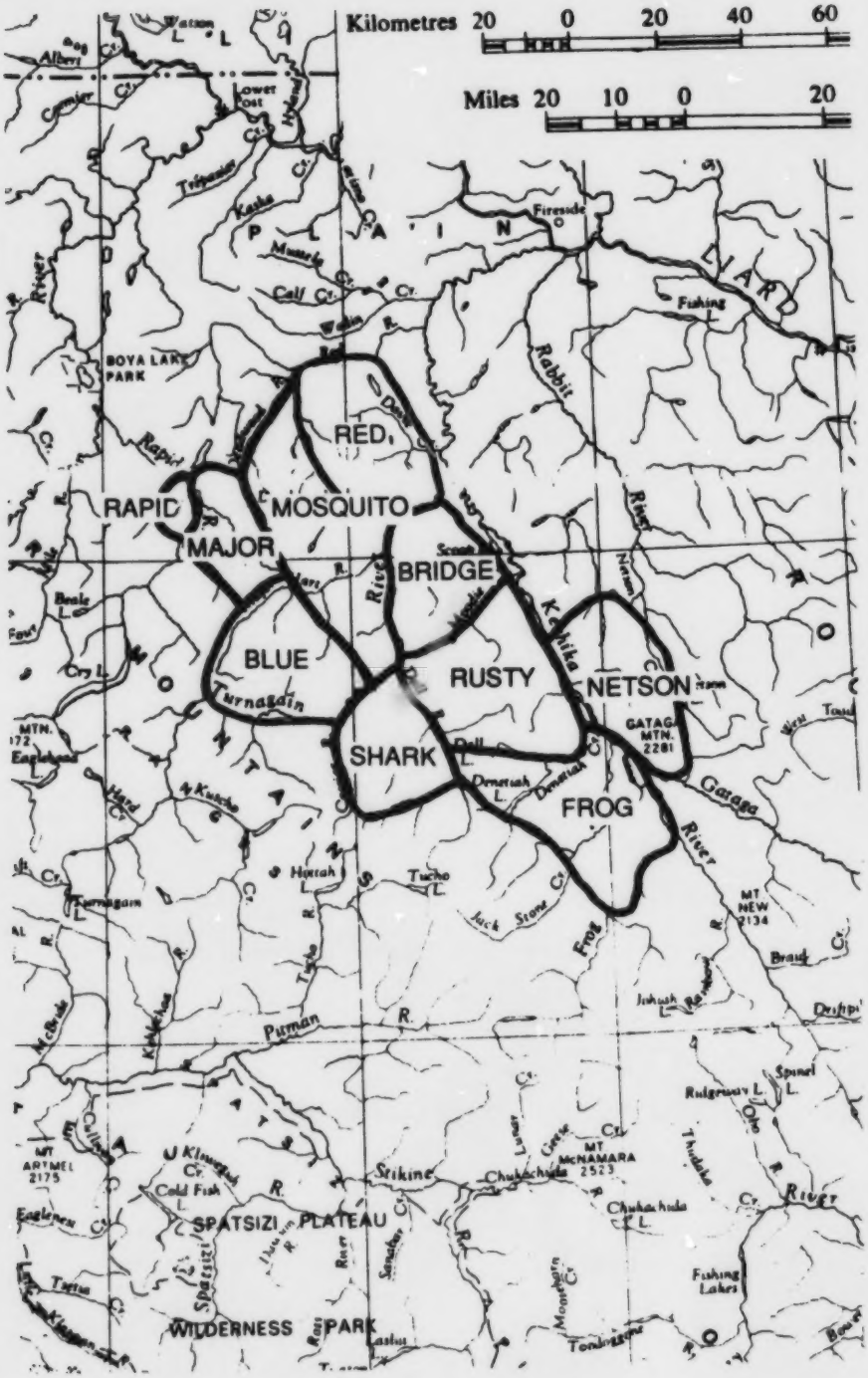


Figure 12. Mountain sheep census areas.

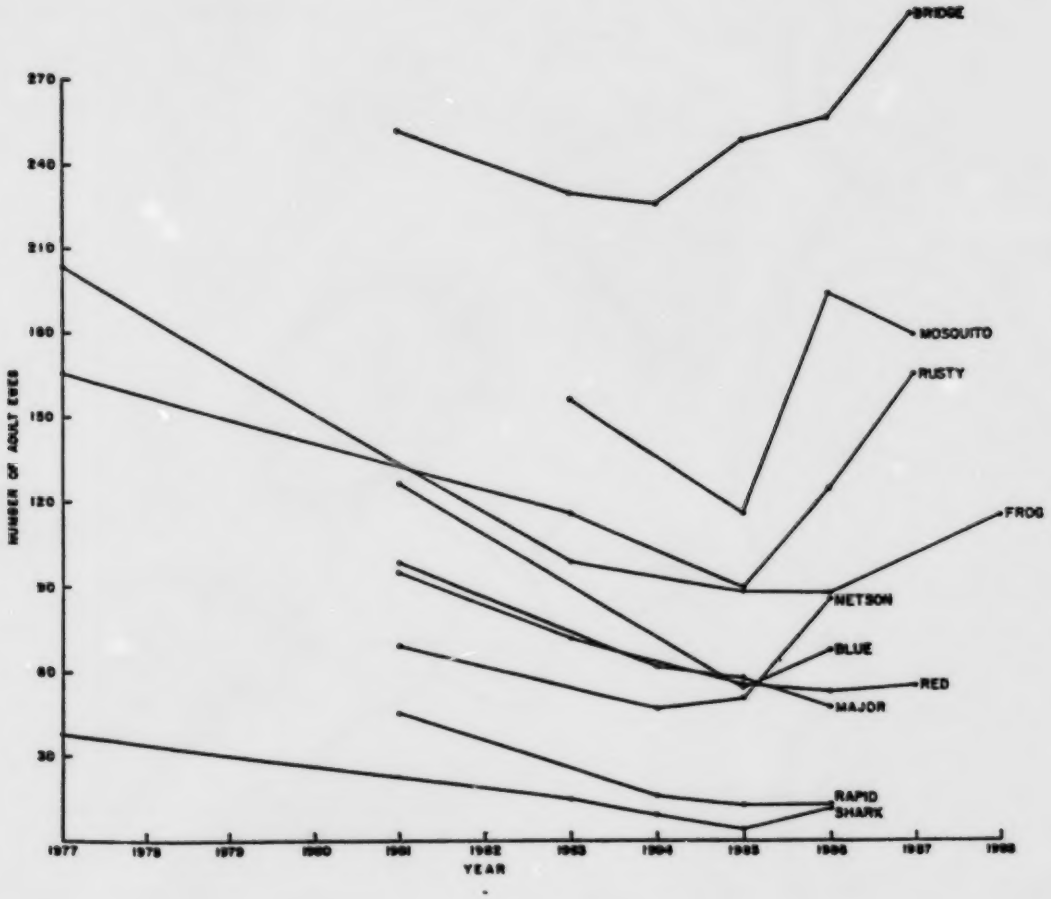


Figure 13. Mountain sheep population trends.

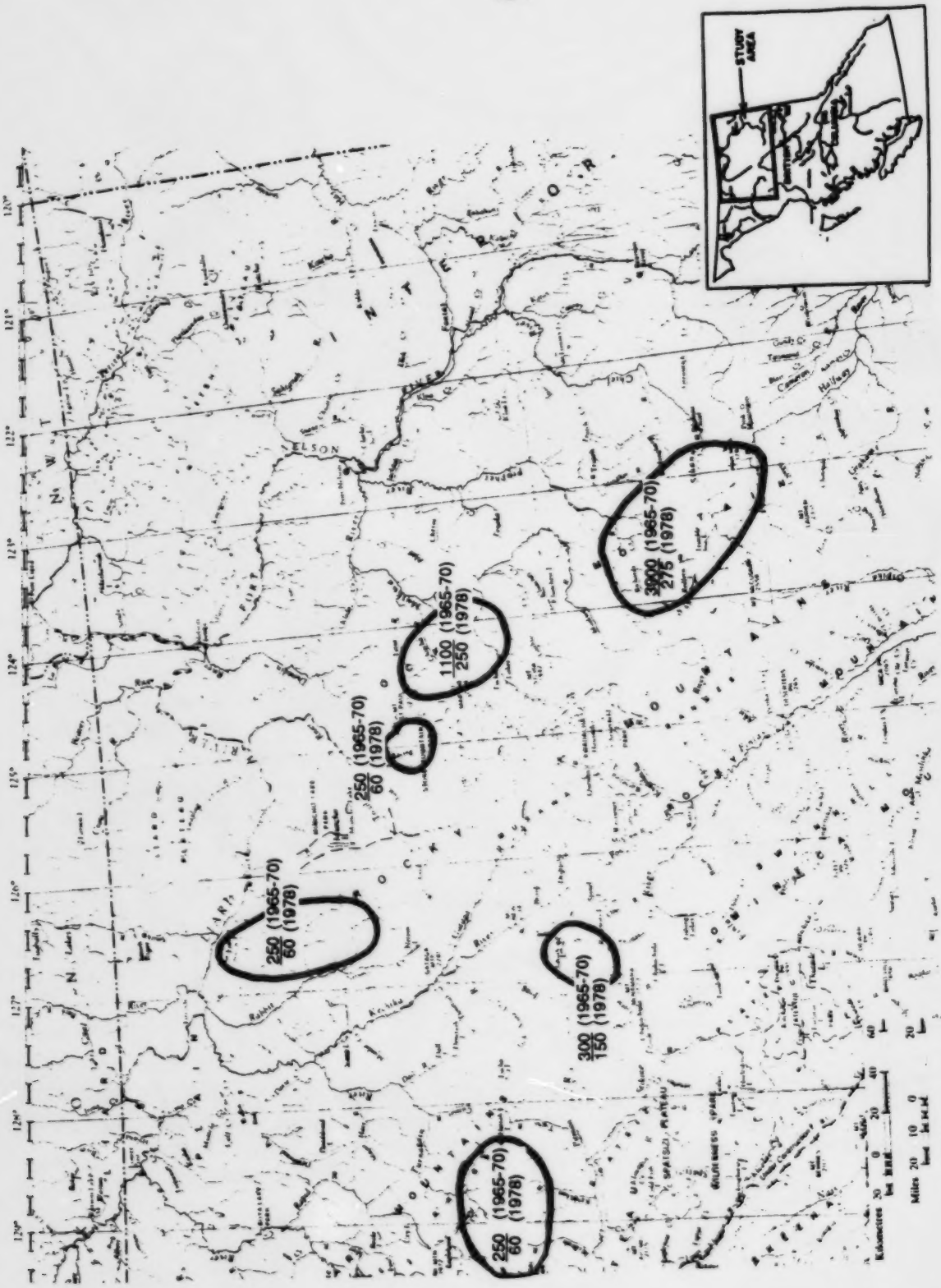
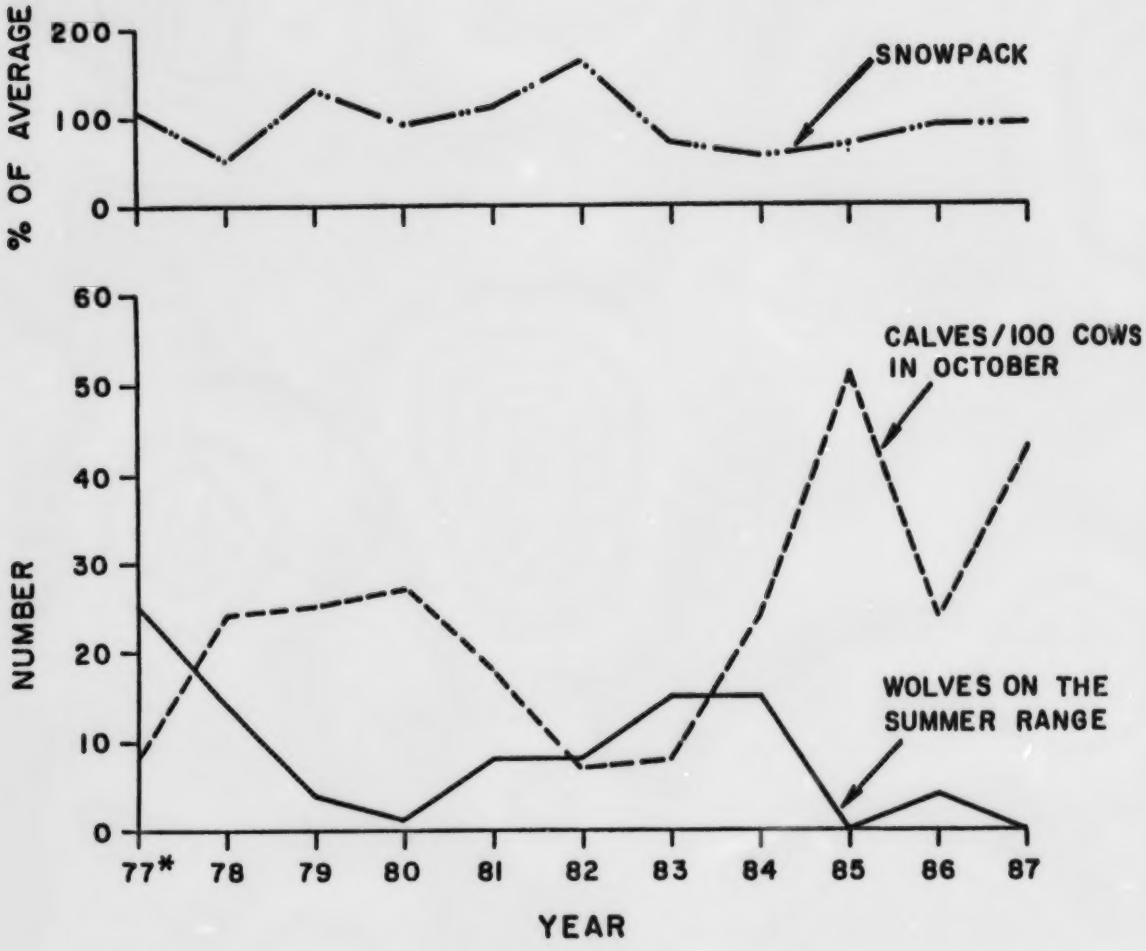


Figure 14. Caribou herd size changes (where known) in northeast British Columbia, 1965-1970 versus 1978. (After Bergerud 1978)



* From Bergerud (1978), 15 caribou calves and 222 adults seen the following 2 years gave 182 and 187 cows, and 37 and 40 bulls, using a similar sex ratio gives 184 cows. The 1978 prereduction level for wolves on the summer range is used for 1977.

Figure 15. Caribou calf production, summer wolf numbers, and previous winter percent snowpack on the Horseranch Range of northeastern British Columbia.

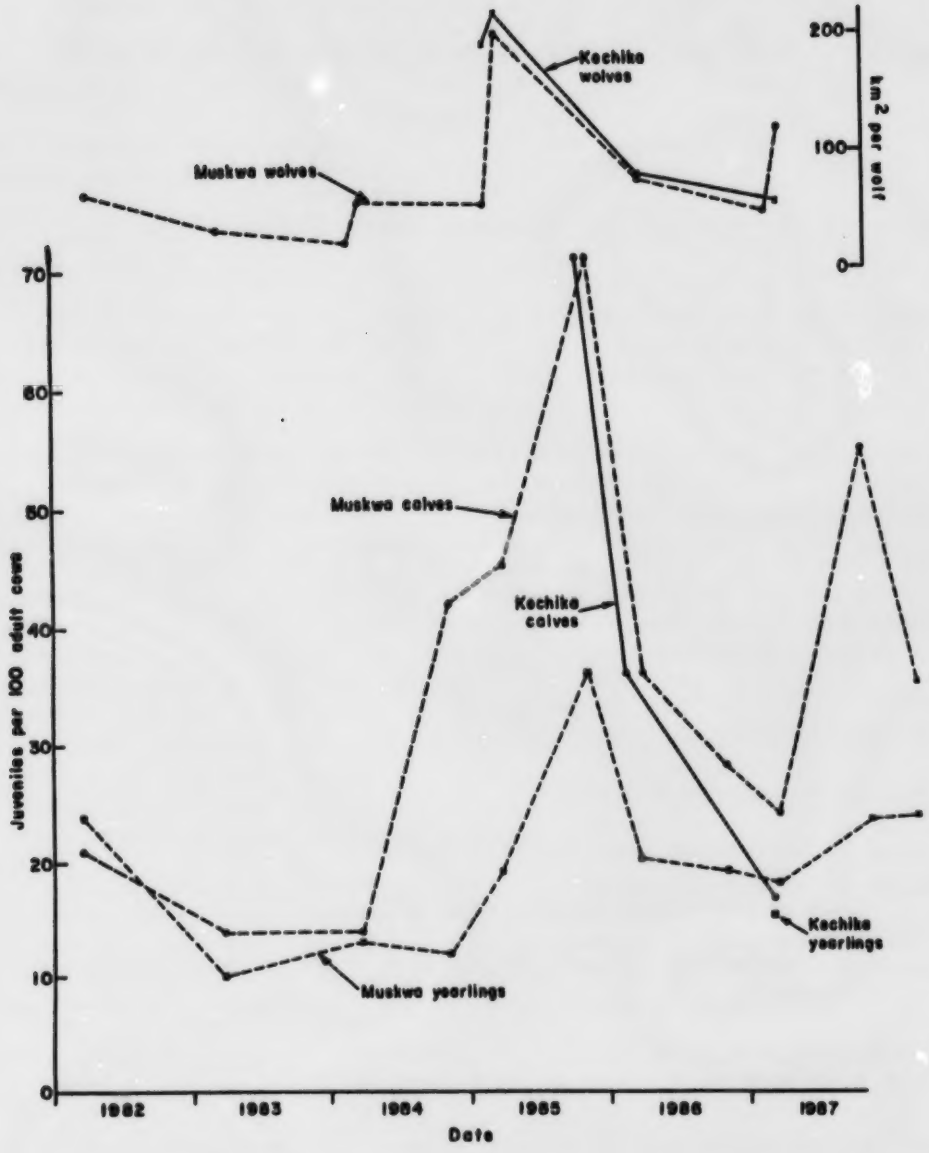


Figure 16. Area per wolf and juvenile survival in elk for the Kechika and Muskwa.

MANAGEMENT OF COMPLEX PREDATOR-PREY SYSTEMS IN ALASKA

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Fairbanks, Alaska 99701

INTRODUCTION

I will discuss predator-prey relationships in a management context; I emphasize management because it is management of predator-prey systems that produces controversy and led to this symposium.

My focus is on systems with wolves, black bears, and grizzly bears as predators and moose and caribou as primary prey. Deer-wolf systems in southeast Alaska are briefly mentioned. I have chosen systems where predators are or were largely lightly exploited; that is, predators were able to more or less seek their own level of abundance. However, there were brief periods of predator control from which we learned about predator-prey relationships.

This paper addresses 3 topics:

1. Why manage predator-prey systems?

2. How predation reduces prey abundance.

3. Management lessons for complex predator-prey systems in Alaska.

I will not dwell on details of individual studies; instead I will use data from several studies to make specific points. Let's begin.

WHY MANAGE PREDATOR-PREY SYSTEMS?

Why manage predator-prey systems? I think the answer is simple--man wants something that unmanaged systems do not provide.

What does man ask from wildlife? How does he use wildlife? For the most part, use falls in 4 four major categories:

1. Viewing and photography--These are major uses of wildlife in Alaska. You only have to look at the flow of people through Denali National Park to realize this. People also extensively use areas outside our parks.

2. Hunting--Hunting for recreation and for trophies is also a major use of wildlife by Alaskans.

3. Food--Wildlife provides sustenance for rural people and many urban people.

4. Spiritual--Spiritual use of wildlife goes far back into human culture and is easily recognized in the totem poles and masks of native Americans. However, wildlife has spiritual qualities for a growing number of urban Americans.

Why are these uses or demands for wildlife sometimes hard to provide? Why must these uses be periodically managed for rather than being by-products of unmanaged systems? The answer is: natural processes sometimes limit prey and predators at low densities. Wildlife at low densities can sustain little use by man--either for viewing or for hunting. Predators play a large role in determining prey abundance, and thus, their own abundance. The consequence of little or no management of predators in predator-prey systems with 2 or 3 predator species is sometimes prolonged low use of wildlife.

Other speakers at the symposium provided examples of predation maintaining prey at low densities in Canada. Let us look at some examples of long periods of low animal abundance in Alaska; predation had a large effect in some of these examples.

Before I present the examples, I want you to realize that I am going to discuss principally predator-prey relationships here. Do not think I dismiss hunting, weather, and nutrition as powerful forces--they are. They play important roles in the dynamics of predator-prey systems. But, because of the short time, I will concentrate on predation.

Let us look at 3 examples where prey populations have declined and remained at low densities for extended periods.

1. Moose abundance in interior Alaska is characterized by long periods of relatively low density during this century (Fig. 1). In eastern Alaska, moose became abundant only after predator control that reduced wolves and grizzly and black bears. Following the cessation of that control, moose rapidly declined to low densities and remained there. Our recent work shows that predation by grizzly bears and wolves maintains moose at approximately 100 moose/1,000 square kilometers.

Moose in central Alaska followed the same pattern, except that following the low-density period during the mid-1970's we again reduced the number of wolves and moose increased (Fig. 1). So, we

can characterize moose populations as commonly fluctuating at low densities relative to their food resources except following predator control.

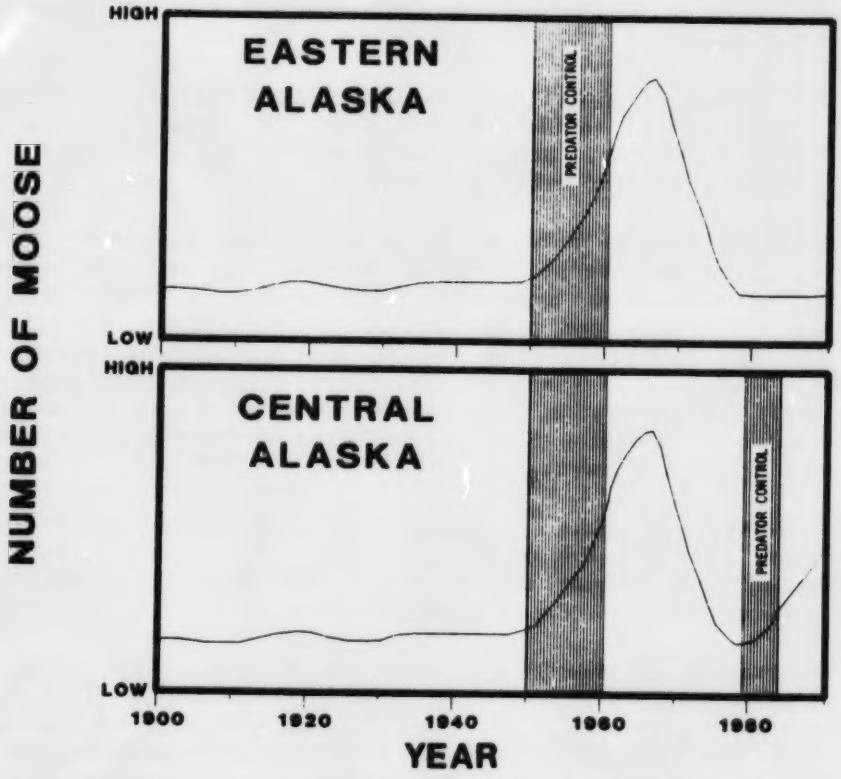

Fig. 1. The relative numbers of moose in eastern and central Alaska from 1900 to 1988.

2. Numbers of caribou in Alaskan herds fluctuate widely and have periods of scarcity (Skoog 1968; Haber 1977). For example, the Denali herd, which lives primarily in Denali National Park, rapidly declined from about 30,000 to about 1,500 caribou by the early 1970's (Fig. 2, Haber 1977; Singer 1987). The herd has remained small for the past 15 years, and though it is increasing, it will likely be small 10 years from now. National Park Service studies indicate predation is an important source of mortality and retards population growth (Adams et al. 1987).

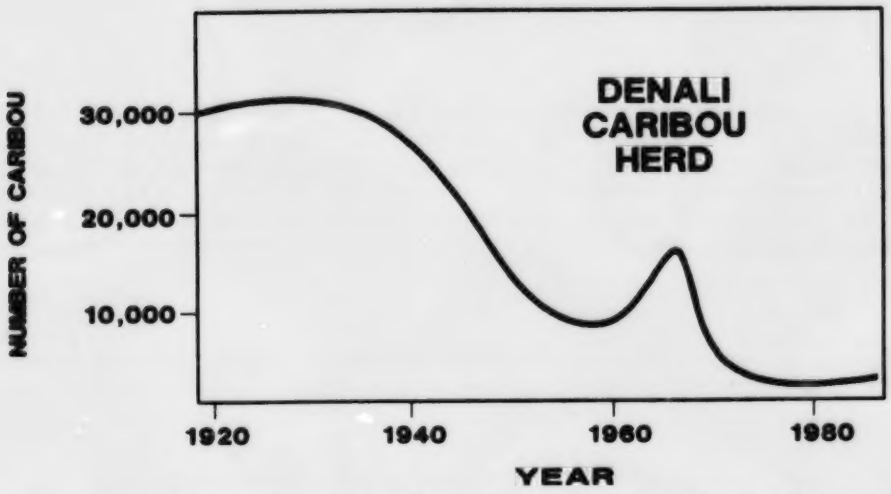

Fig. 2. The approximate number of caribou in the Denali caribou herd of Denali National Park and Preserve from 1920 to 1987, Alaska (Haber 1977; Singer 1987).

3. Deer in coastal southeast Alaska fluctuate with weather and predation (Merriam 1970; Olson 1979). While there was predator control, deer fluctuated fairly synchronously on islands with and without wolves (Fig. 3), although peak densities may not have been as high where wolves were present. But with the cessation of predator control in 1960, deer populations did not rebound from the severe winters of the late 1960's and early 1970's on some islands with wolves, and recovery has been delayed on other islands with wolves (Smith 1987; M. Kirchhoff and K. Pitcher, unpubl. data). Where wolves were absent, deer populations rapidly rebounded and are now at high densities. Wolves declined in abundance with the reduction in prey (Fig. 3).

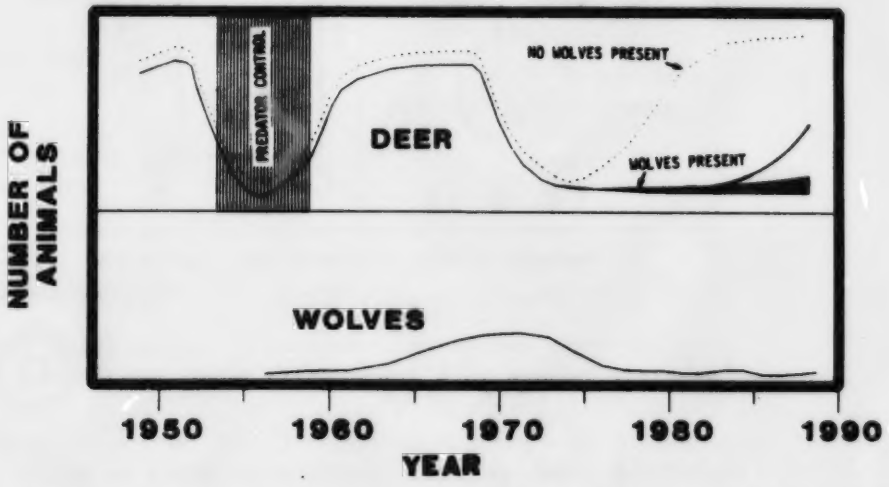

Fig. 3. The trends in deer and wolf abundance on islands with wolves present (solid lines) in southeast Alaska, and the trend in deer abundance on nearby islands without wolves (dotted lines).

These examples show that, at times, unmanaged systems have low prey and predator densities. Low-density populations provide little recreation, food, or spiritual use. Sometimes predation is a major cause of prolonged prey scarcity.

HOW DO TWO OR THREE PREDATOR SPECIES MAINTAIN STRONG CONTROL OVER PREY POPULATIONS?

I will point out 3 of the ways predators cause prey populations to decline and/or remain at low densities.

1. Predators can kill a large proportion of the population annually. For example, Fig. 4 shows the number of moose dying from various causes in a low-density moose population in eastern Alaska. A population of 1,000 adults and yearlings produces about 670 calves, most of which die from predation. Predation is also the most important cause of mortality for adults and yearlings, followed by hunting and miscellaneous causes. By summing all the deaths in the population, we find that predators killed about one-third of the population annually. Other natural causes killed about 5% of the population, and hunters killed about 2%. Clearly, predation is a powerful force on the population.

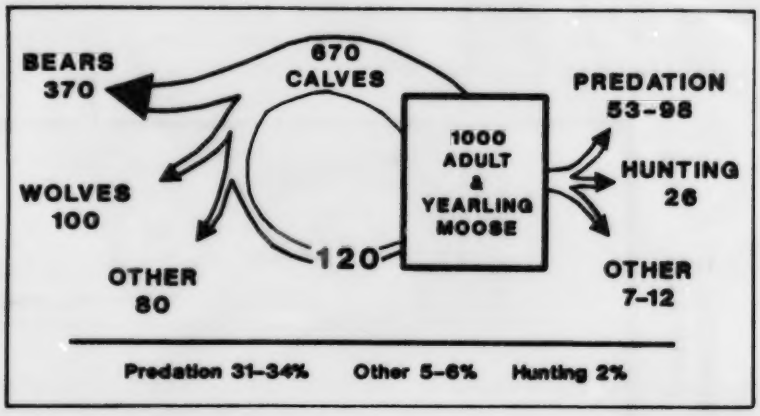

Fig. 4. The approximate numbers of moose dying from specific causes in a low-density moose population in eastern Alaska.

2. Mortality from predation is largely added to other sources of mortality when prey have abundant food resources. Predation does not simply replace other forms of mortality by taking animals that are about to die. Predators kill many animals that would have lived and reproduced. Predator reduction experiments demonstrate this. Survival of moose and caribou markedly improved following wolf control (Table 1).

Table 1. The percentage of moose and caribou surviving annually when wolves were abundant before wolf control and when wolves were scarce after wolf control in central Alaska during the 1970's (Gasaway et al. 1983).

	Annual percent survival	
	Wolves abundant	Wolves scarce
Calf moose	15	50
Adult moose	80	94
Calf caribou	7	56

This increased survival resulted in population growth of moose and caribou (Fig. 5). Wolves also increased when we stopped control; now predators and prey are abundant.

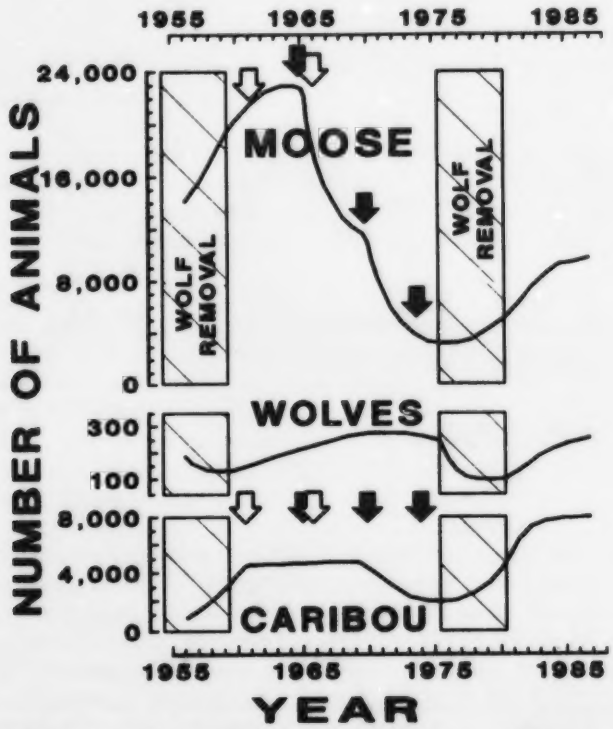

Fig. 5. The approximate numbers of moose, caribou, and wolves in a central Alaska management area (Game Management Unit 20A; updated from Gasaway et al. 1983). Open arrows indicate moderately severe winters and solid arrows indicate very severe winters.

Predation often results in additive mortality on the prey population--reduce that mortality and the prey population will increase at a faster rate.

3. The last point is that predators and predation do not rapidly decline as prey decline; predators lag behind their prey. For example, in our eastern Alaska study, the decline in wolf numbers lagged behind the rapid decline in moose and caribou numbers from the mid-1960's through the mid-1970's (Fig. 6). Wolves remained abundant until both moose and caribou declined to low numbers. Other examples exist in Alaska and on Isle Royale.

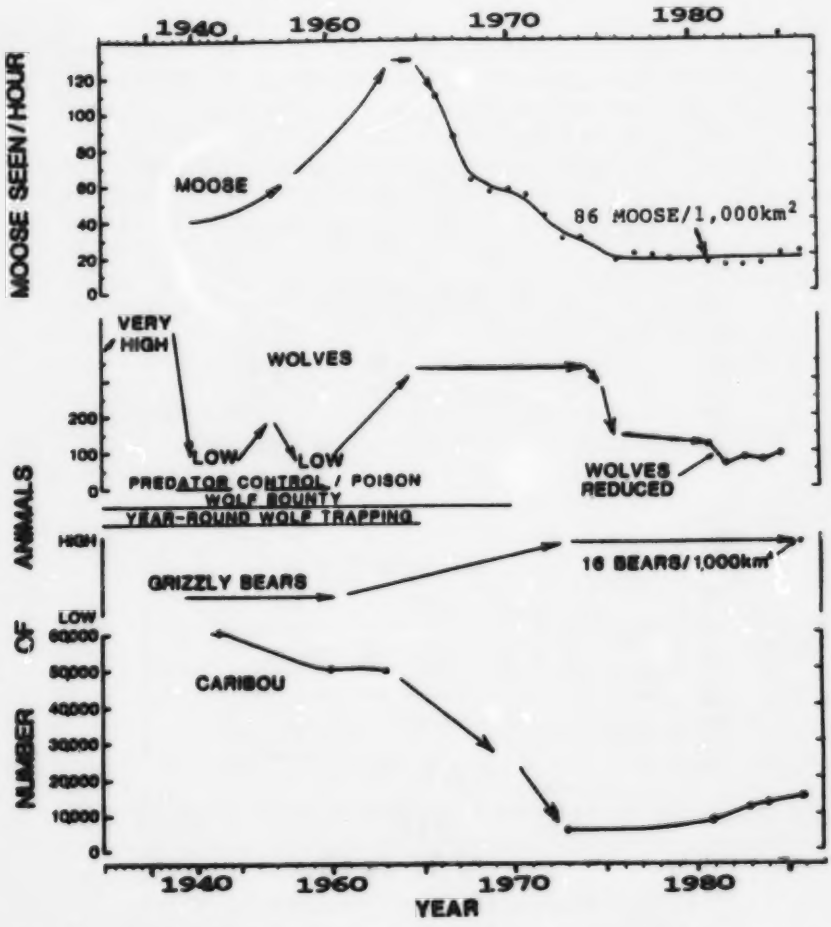

Fig. 6. The approximate numbers of moose, caribou, grizzly bears, and wolves in an eastern Alaska management area (Game Management Unit 20E) (Gasaway et al. 1988).

Unlike wolves, bears can remain abundant long after ungulate prey decline to low densities. Bears are not dependent on moose and caribou, as are wolves. Instead, bears rely a lot on vegetation. However, the impact of bear predation can be high on low-density prey populations because grizzlies can maintain a high kill rate even when prey are scarce. Data from 2 studies in Alaska demonstrate this point. Radio-collared grizzlies killed 1 moose calf per 7 days during spring where moose calves were scarce and killed at the same or slightly lower rate (1 calf per 8-12 days) where calves were several times more abundant (Ballard et al., in press; Boertje et al., in press).

To summarize, predators sometimes cause prey populations to decline or remain at low densities because (1) predators kill a high percentage of the population; (2) mortality from predation is partly additive, that is, it does not fully substitute for mortality from other causes; and (3) predation persists at high rates during and after prey decline.

MANAGEMENT LESSONS FOR COMPLEX PREDATOR-PREY SYSTEMS

In this section I will discuss some of the important management lessons we have learned in Alaska.

1. Do not let prey decline to low densities before deciding to manage if moderate use of wildlife is a goal. Procrastinating may cause prolonged low prey and wolf densities and little wildlife use. Some of the management problems that intensify as prey decline are:

A. The effects of predation on low-density, declining prey populations may increase on the short term. Wolves can remain abundant during the prey decline, and bears may become the major predator at low prey densities. To increase moose populations, for example, predator numbers may have to be severely depressed and both bears and wolves may have to be killed.

B. Wolves will eventually become scarce when prey decline to low densities. For example, with low prey densities in Denali National Park, wolves number only about 5 per 1,000 square km (Singer and Dalle-Molle 1985). Dave Mech told me that wolves are having a difficult time making a living in the low prey environment, based on his wolf study in Denali. In contrast, wolf density is nearly 3 times greater (13-15 per 1,000 square km) in an adjacent managed area with abundant prey. There, we reduced wolf numbers from 1976 to 1981; the low wolf density during the control period was similar to the present wolf density in Denali National Park. Thus, wolves can be fairly abundant in managed areas.

C. Recovery of low-density prey populations may require many years and intense, long-term predator control. For example, moose in eastern Alaska have been scarce (about 100 per 1,000 square km) for nearly 15 years (Fig. 7). Today, if we alter the system enough to get a 5% annual increase, moose would still be scarce 15 years from now. That is 30 years at low moose densities--a long time in a person's life, though short on an evolutionary scale. Rapidly raising moose densities to where moose are common or abundant requires about a 20% annual growth rate or a population doubling time of about 4 years (Fig. 7). That almost certainly requires a severe, prolonged predator control program, which we all want to avoid. Therefore, consider managing predator-prey systems while prey are still common.

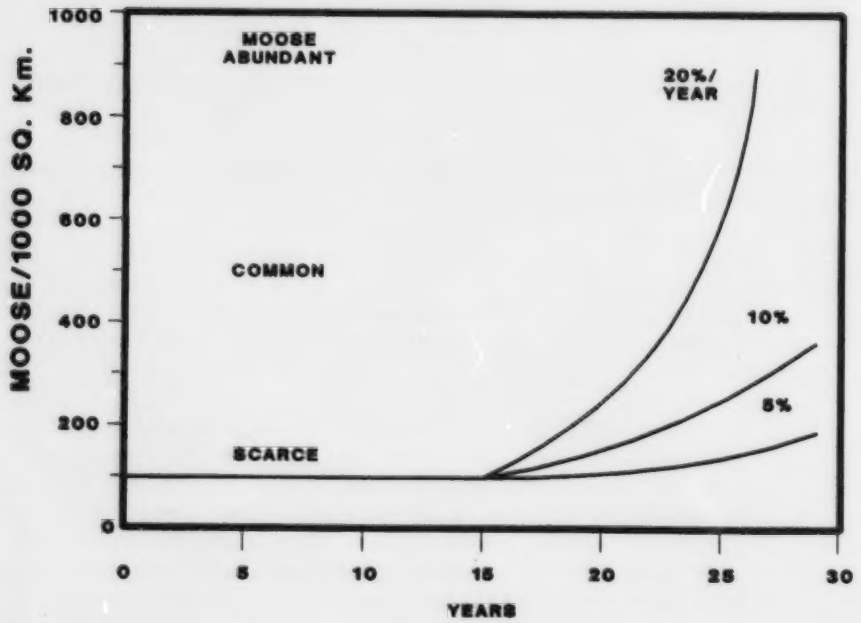

Fig. 7. When starting at a low moose density, many years are required for moose to become common or abundant unless the annual rate of increase is near 20%. Moose density is shown for 5%, 10%, and 20% annual rates of increase starting at year 15.

D. The last point is that wildlife helps preserve wildlife habitat and wilderness. By this I mean scarcity of wildlife opens the door to competing forms of land use. Abundant wildlife and its use can be a strong bargaining chip when arguing for rational timber, agricultural, and industrial development and retention of wildlife habitat. For example, during the early 1970's, the presence of 300,000 caribou altered oil development in Alaska's arctic. Had only a few

thousand been present at that time, development of the oil field and pipeline probably would not have accommodated wildlife as well. Today there is an intense debate over extracting oil in the Arctic National Wildlife Refuge, the calving area for the Porcupine caribou herd. Those 180,000 caribou are the major bargaining chip for retaining it as wilderness.

Other examples occur in southeast Alaska where deer are central in the argument for retaining old-growth forest, essential habitat for many wildlife species. When deer become scarce our wildlife agency has more difficulty arguing to maintain old-growth forest. I am sure it is the same in British Columbia.

2. On the long-term, prey and wolves will not remain abundant in the absence of long-term management. In other words, there is no long-term high equilibrium in some predator-prey systems. Moose in eastern Alaska serve as an example (Fig. 2 and 6). Moose increased to high densities following predator control, thus giving the system the opportunity to establish a high equilibrium. However, moose, caribou, and eventually wolves declined to a low density. Moose density is now about 100 per 1,000 square km, a very low density. Our studies show predation prevents moose numbers from increasing. This pattern of increase and decline occurred in much of interior Alaska, in hunted and unhunted areas. Therefore, long-term management is required in some areas to maintain wildlife at moderate densities.

3. Numerically, wolf populations recover rapidly from predator control. Data presented by John Elliott at this symposium showed recovery periods of 2 to 3 years in British Columbia. In Alaska, wolf populations usually recover in 3-6 years. However, socially, wolf populations are highly disrupted by predator control; social recovery probably takes much longer than numerical recovery.

4. Predator reductions have worked effectively to manage complex predator-prey systems in Alaska. Benefits have been increased prey, wolves, and recreation. For example, wolves, moose, and caribou are at low densities in Denali National Park compared with an adjacent management area where predator numbers were periodically reduced (Fig. 5). As previously mentioned, wolves in the managed area are now about 3 times the density in Denali Park. Earlier today, Dale Seip suggested it may be possible to raise long-term wolf densities if prey numbers are increased through wolf control. This clearly can be done and is being done in parts of Alaska. Increasing wolf abundance is a goal in portions of Alaska. The wolf is a highly valued species.

Reducing predation through lethal predator control programs is unpopular to the majority of people and is divisive. Hence, we are investigating new, nonlethal means of manipulating predator-prey systems in more socially acceptable ways. Several alternatives hold promise.

5. The last lesson is to allocate shares of prey to predators and man in written management plans. This assures people that predators have a long-term place in the ecosystem and shows how man, wolves, and bears will share prey. The flow chart in Figure 4, for example, quickly shows all concerned how the moose resource is shared in a portion of eastern Alaska. There is no mistaking that bears and wolves are allocated most of the moose resource; one-third to predators and 2% to man. A flow chart such as this helps clarify current or future allocation decisions.

CONCLUSION

I will conclude with 4 points.

1. Predator-prey management is necessary in many systems to sustain the long-term desires of people. The reason--natural processes sometimes cause wolves and their prey to become scarce for long periods. Low wildlife densities provide for little use. If predator-prey systems commonly remained at a high equilibrium, then we could manipulate them and forget about intensive management for decades. That doesn't seem to be the case.

2. Do not wait until prey are at low densities to begin managing predator-prey systems. Recovery of prey and wolf populations can take a long time and require severe management actions.

3. Predators can be abundant in exploited systems. I have given you examples in Alaska. Man can share prey with large predators without driving predators to prolonged low densities.

4. Lastly, I want to stress that abundant wildlife helps preserve wilderness and large carnivores. By maintaining fairly abundant wildlife, we can more effectively argue for preserving wildlife habitat, and especially wilderness. Without wilderness, few wolves and grizzlies will survive.

Management of large carnivores has become a battle ground among conservationists. We have become so polarized that we no longer stand together on the more important issues. It is time to unite! It is time to respect our ethical differences regarding wildlife use and get on with ensuring a long-term place for wildlife in North America.

Let's not give our wildlife habitat to industry, agriculture, and urban sprawl because we temporally let our large ungulates and carnivores decline to low densities and lose their competitive value in the race for land uses.

If we can preserve the ungulate-carnivore systems and the wilderness they require, then there will be plenty of wildlife for viewing, hunting, and spiritual use.

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THE IUCN/WWF PERSPECTIVE ON WOLF CONSERVATION

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As I understand it, my job this morning is to review for you the IUCN and WWF position on wolf conservation. In a sense, that's easy, because IUCN's perspective *is* WWF's perspective.

For those of you who may not know, *World Wildlife Fund* is a network of 23 national organizations, founded in 1961, which has raised about $500 million for 5000 projects in 130 countries. I'm President of the Canadian national organization, founded in 1967, which has supported about 700 projects worth $35 million since I arrived 10 years ago. We're probably best known as that organization with a prince for a President and a panda for a logo, because Prince Philip spends about 1/3 of his time heading up our international activities, and the Giant Panda logo represents endangered species and habitats which have constituted the top-priority for WWF's work.

IUCN is the *International Union for the Conservation of Nature and Natural Resources*, founded in 1946, today representing over 500 government and non-government organization members and some 5000 scientists world-wide organized into 6 commissions. IUCN is housed in the same building as WWF International in Switzerland, and forms a kind of sister group giving scientific direction to the fundraising clout of WWF.

The Species Survival Commission of IUCN is made up of a number of specialist groups, including an international Wolf Specialist Group now chaired by Dr. David Mech from the North Central Forest Experiment Station in Minnesota. The Wolf Specialist Group has drafted two documents of direct interest to us today, which I have circulated in case you don't already have a copy. The first is the *Manifesto and Guidelines on Wolf Conservation*, drafted in September, 1973 under the chairmanship of Dr. Douglas Pimlott, subsequently endorsed as the official IUCN position on this subject and published in the IUCN Bulletin in May, 1974.

The second document is called *Accepted Changes in the Manifesto and Guidelines on Wolf Conservation*, reviewed by the Wolf Specialist Group in

August, 1982, endorsed by the Species Survival Commission in January, 1983, and subsequently accepted by the IUCN Council in the same year.

Finally, I have enclosed a 1984 statement on wolf control signed by David Mech on behalf of the IUCN Wolf Specialist Group because I think it's important to the deliberation of this symposium.

Sorry for running over what I'm sure is familiar ground to most of you, but I want to make sure we've all got a shared information base, actually out there in your *hands*, so that it's crystal clear what I'm talking about.

I must also confess one rather personal point, mentioned by Lu Carbyn, again in case you don't already know. I was a close friend and great admirer of Douglas Pimlott, first Chairman of the IUCN Wolf Specialist Group. My wife, Marion, worked as a research assistant with Doug. I worked with him for 15 years on various conservation issues in Ontario, as a professional colleague because we team-taught the undergraduate course in Environmental Studies at the University of Toronto for 5 years, and as a co-worker in the field. I considered it a great honour, at Doug's request before he died of cancer, to organize and speak at his memorial service in September, 1978, coincidently my first day on the job at WWF. Many, many people were touched by Doug. Many of them are in this room. He was a great Canadian. Apart from being the world authority on wolves during his time, he stood for fairness and integrity in everything he did. In fact, when faced with difficult decisions, to this day I find myself asking, "What would Doug have done?"

And *that's* the measuring stick I've tried to use for my remarks today. Faced with his original Wolf Manifesto, the changes made to it after his death, and the roster of existing and proposed wolf control programs in Canada today, what *would* Doug have said? It's a fair question, I think. It's also a daunting one, because I'm not trying to set myself up as some kind of posthumous spokesman for Doug Pimlott. Further, Doug often told me that within his lifetime he felt many of his students overtook him in their knowledge about wolves. So in this sense, it may not really *matter* what Doug would have thought, because he was so willing to hand the torch to others. And I want to emphasize that many of these people, many of *you*, many of *us*, *with absolute personal integrity and based on the best science available*, now find ourselves on different sides of the wolf control question.

To get to the point, I think Doug would say that the original Wolf Manifesto has clearly been pushed from a fundamentally protectionist document, arguing for

appreciation of the wolf as a natural predator with a right to exist entirely unrelated to its known value for mankind, to a document more sympathetic to management concerns. I hope no one familiar with the IUCN documents I've handed out would seriously argue with that, and for those of you who haven't read them, take a look and you will see what I mean.

There is really only one clause of the original Manifesto, Number 7, which even *mentions* wolf control , and it reads:

> "Where wolf control measures are necessary, they should be imposed under strict scientific management, and the methods used must be selective, highly discriminatory, of limited time duration and have minimum side effects on other animals in the ecosystem."

Similarly, there are only two references in the original Guidelines, one to "zones within which wolf numbers would be regulated according to ecological principles," and another prohibiting "poisons, bounties and sport hunting using mechanized vehicles". Presumably what applies to sport hunting would also apply to government control programs, and mechanized vehicles would include aircraft.

The other 11 clauses of the 1974 Manifesto, and the other 72 points made in the original Guidelines on Wolf Conservation make no reference whatsoever to wolf control and emphasize a more appreciative or protectionist viewpoint. It would take the rest of my talk to cite all these, so I won't.

The 1982 changes to the Manifesto, however, preoccupy themselves *entirely* with Clause 7, elaborating on the conditions under which wolf control is acceptable even in endangered wolf populations, and arguing for public education programs which are "factual, professional, realistic and accurate", as if the original guidelines were somehow deficient in this respect.

David Mech's 1984 statement takes the IUCN position even further into the management camp, pointing out that wolf control under certain circumstances *can* substantially increase prey numbers, and that it really isn't the purview of IUCN to comment on such programs unless a given wolf population is endangered. He further argues that although such programs should be based on scientific principles, "it may not always be possible, feasible, necessary or desirable to wait until a completely definitive study is conducted in each

instance before control is instituted". In this regard, I remind you that Pimlott's original document stated *categorically* that wolf control should *only* be imposed "under strict scientific management."

So my argument - I think completely supported by the documents them*selves* which are in your hands - my argument is simply that the original IUCN Wolf Manifesto has been progressively softened by subsequent changes - sometimes subtly, sometimes very obviously - to move it towards making wolf control more and more acceptable.

The result, of course, is that those who take a more protectionist stance select those aspects of the Manifesto which support their position, as do those who want an international endorsement for wolf control. In short, we have a classic IUCN document which sits squarely on the fence, comfortably harboring potentially contradictory viewpoints. As they used to say in the sixties, we are left wondering whether this thing "oinks or moos".

And that, ladies and gentlemen, is pretty much the nature of IUCN and WWF's official position on wolf conservation. As such, I suppose that is really about all I'm authorized to say as an official spokesman for either WWF or IUCN. Therefore, at this point I should probably fold up my notes and, sit down having given a relatively safe presentation on a controversial topic.

But then I wouldn't have done what I promised to do, which is to answer the question, "What would Doug Pimlott have thought of all this?"

So far, I've simply said he would have judged that the IUCN position has been pushed more and more towards a wolf control/wolf management position. But let's face it, the really *interesting* question is, "Would Doug have *approved* of this?"

Well, in my view, *he* definitely would not. And that is all the words I care to put into Doug Pimlott's mouth. From here on it's strictly Hummel speaking.

Building on what I take to be the major thrust and original intent of IUCN's Wolf Manifesto, I would like to suggest a kind of decision tree, three key questions or hurdles which must be addressed on the whole question of wolf control. Incidentally, by wolf control, I mean relatively large scale interventions into wolf populations to increase wild prey numbers for human purposes. I'm *not* talking about small scale control of problem individuals to protect livestock or endangered species.

First question: *How sure are you that the wolf is the major limiting factor on a given prey species?*

High school biology teaches us that a number of factors can limit an ungulate population, including weather, snow depth, nutrition, parasites, natural range condition and people-oriented factors such as habitat alteration and hunting pressure. Nearly everybody mentioned this yesterday, and I felt Doug Janz's experiment on Vancouver Island particularly showed the difficulty in separating out confounding background variables. The cold, political fact, of course, is that we can't control the factors attributable to Mother Nature. And we don't *want* to control human factors. So by a process of elimination, the wolf ends up being the easiest button to push. *But*, let's assume for the sake of argument, that you have passed this first hurdle, that in a politically neutral environment it can be scientifically shown that wolves *are* indeed the primary limiting factor on a given prey population, which incidentally I personally *do* believe to be true in many cases.

Second question: *Will pressing the wolf button have the desired effect, and for how long?*

This is really a question about the predictability of management intervention. In the *short* term, in some cases, I agree we have evidence that suppressing wolf numbers will result in, say, improved survival and recruitment of calves. But it can also stimulate compensatory natality on the part of wolves or because of ingress, result in a marked rebound in their numbers in the face of abundant prey. Data presented by Messier, Hayes, Elliott, and Gasaway all confirmed this fact. Therefore, to maintain the artificial imbalance between predator and prey being sought by humans, *repeated* wolf control is likely to be necessary. In this regard, I whole-heartedly agree with John Elliott that "pulse-management" has proven a waste of time, leaving him with two choices: either steady, continuous control, or no control at all. But once wolf control is initiated, you may well be hooked on management. Therefore, I think it's fair to ask, has this been clearly budgeted for and explained to the public?

I suggest that such interventions, put in the perspective of long-term predator/prey relationships, will have a short-term effect at best, which causes me to ask about the real merits of starting such programs in the first place. I must also say that I personally feel we rarely understand the consequences of large scale interventions into *any* natural system, primarily because we don't really understand long-term natural relationships in general. Rick Page

cautioned us not to use 3 or 4 year blips on the graph to characterize long-term predator-prey relationships. But only he and Lu Carbyn produced data sets extending beyond 10-15 years. The only other reasonably long-term research I know of is in Algonquin Park, and ironically these long-term studies are precisely what WWF must support in Canada because Governments will not.

But, again for the sake of argument, let's say you have passed Tests Number 1 and 2, that is, you can reliably separate and identify wolves as *the* most important limiting factor, and you can reliably predict the result of a large scale wolf control program, at least in the short-term.

Third question: *Is it ethically justifiable to manipulate wild populations to ensure that human predation can be maximized?*

Many people tried to ask this question in different ways yesterday. Now, of course, I've skated from the scientific end of the rink onto the ethical side. But I want to make it clear that I don't think you have to come at this from an anti-hunting point of view. I'm not arguing that sport hunting is wrong. In fact, I was raised in the bush and personally earned a fair bit of pocket money from guiding. No, I'm really asking about the nature of the hunting experience itself. You see, I was always taught that predators, human or otherwise, have good years and bad, depending on the relative abundance of prey. Some years you have a good duck hunt; sometimes the pickings are pretty lean. Some years you get a deer or moose; some years you may get none.

My point is that the experience of scarcity and lack of success is part and parcel of true hunting. So it is for the wolf. But unlike us, the wolf starves, or otherwise compensates by controlling its numbers. *That's* reality. *That's* natural. It's *un*real and *un*natural for every year to be a good one. In fact, it's not true to the experience of hunting to eliminate your natural competition so that prey species are so abundant that you virtually cannot fail. No other predator does this. Why should we? Some say we are entitled to do this simply because we *can*, and more important, because money and jobs are involved.

Bill Gasaway says we should do it because we want things that unmanaged systems don't provide. He urges us to produce more wildlife than is found in unmanaged systems, so we can outcompete industries who want to exploit wildlands. More caribou means keeping the oil and gas industry out of the Arctic International Wildlife Range. More deer or woodland caribou mean keeping the forest industry out of old growth. Let's stop fiddling over our petty

differences while Rome burns, says Bill. Let's join hands to protect wilderness by controlling predators.

I say go easy. First, most people support wilderness proposals precisely because large predators are *protected* by it.

Second, I'm not yet ready to concede, even in B.C., that the only natural systems we can realistically protect are those heavily managed by people. In fact, I'm not sure that's wilderness at all.

Third, the primary reason for controlling predators is not to protect wilderness, *but to create a surplus of ungulates for human predators*, and such programs should be evaluated on that basis.

I'm not saying we *can't* work together, Bill, but if it's a marriage of convenience, let's be honest about it.

Let me conclude on a conciliatory note, because I realize I may have been a little provocative today. First, I have questioned my own organization's position on wolf conservation. Second, I have put words into Doug Pimlott's mouth and may have hurt some people who also consider themselves admirers of his and every bit as familiar with Doug's philosophy as I am. Third, I'm not suggesting that anyone who disagrees with me is less than honest or misguided. But I *do* think we should be more forthcoming when wolf control is really put forward as the best position which could be expected given certain political realities, versus what is biologically and ethically justifiable in the best of all worlds. Don't you wish we *had* the best of all possible worlds? Incidentally, this is precisely why Doug Pimlott left government service for the academic community where he felt he could speak his mind more freely, and he did.

I guess what I'm really trying to say is that I may well be wrong. But I have tried to be honest with you in my assessment of IUCN's position, and where I think we go from here. I believe the IUCN Wolf Manifesto, especially as amended, *equivocates* on the question of wolf control. In the end, it throws the question back to us, asking us to exercise our best judgement and to simply be honest with ourselves. And maybe that is *exactly* how the original drafters intended it.

SOME PUBLIC PERSPECTIVES ON WOLF CONTROL

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It's often been said that the longest journey begins with a single step. Well, I took my first step into the labyrinth of the wolf management issue as a concerned member of the public ... the same general public that forms the basis of this presentation. A few key individuals -- in particular, the late Dr. Pimlott's work, what he stood for and his vision for the wolf -- inspired me to step somewhat boldly. I now represent Northwest Wildlife Preservation Society, an educational public interest group which came to life over a year ago with the intention of addressing the wolf -- and wildlife -- management in B.C.

When we began to investigate and research the wolf issue, we were amazed at the conflicting attitudes that prevailed. We were also overwhelmed by the concern and the interest shown by the public at large, particularly on the subject of wolf control. We spent more than a year listening to many perspectives, talking with many specialists in their fields, reading, researching, publishing, educating, and even joining the Wildlife Branch on a caribou-wolf survey.

We are presenting today a summary of some public perspectives that have surfaced throughout the year, many of which have been confirmed by a survey that we undertook recently to throw some light onto how the public feels about wolf control. We sent questionnaires out to as random a sample of British Columbians as our resources permitted. We did not mail them to our members nor did we use mailing list(s) from any public interest groups. We received a 40% return on a total of 1,000 questionnaires that we distributed -- clearly illustrating that this is an issue of great concern to the general public. (And we didn't even provide them the luxury of stamped, self-addressed envelopes!). I won't go into the details of the survey questions, as copies are available to anyone who would like them. I would prefer to focus on the results.

Our survey respondents were from 18 to 77 years old, with an average of 34. Eighty-four percent of them lived in cities, with the rest spread out over towns and the country. Some respondents were students, followed by business people (those in sales, office work, etc.); labour and trades; professionals, such as doctors and lawyers; and educators. The resource industry respondents consisted of people directly involved in mining, forestry, wildlife, wilderness, or biology; and the hunters included fishermen and trappers.

AGE:	Low.....18	RESIDENCE:	City..... 84.7%
	High.....77		Town..... 9.7%
	Average...34		Country..... 3.8%

OCCUPATION:	Student.....28.0%	Educator.....5.4%
	Business...15.3%	Resources.....5.6%
	Labour.....14.8%	Hunter/Fisher...3.3%

In other words, this sample is fairly representative of B.C.'s overall provincial population in general: a high proportion of city dwellers; an average age in the 30's; and spread out over these occupations. This survey after all represents what the general public thinks about wolf control, not just what special interest groups think.

In answer to our first question,

"DO YOU FEEL THE FUTURE OF B.C.'S WILDLIFE, IN WILDERNESS, IS SECURE?"

85% of the respondents answered "NO".

Of this group, in response to our question:

"DO YOU CONSIDER YOURSELF WELL-INFORMED ABOUT B.C.'S WILDLIFE?"

70% responded "YES".

Survey respondents were asked to provide their own answers to our question:

"WHAT DO YOU BELIEVE ARE THE REASON(S) FOR WOLF CONTROL?"

The highest number of respondents said

"FOR THE HUNTING COMMUNITY AND /OR RELATED ECONOMIC GAINS".....40.6%

Others felt it was

"TO PROTECT UNGULATES.....13.0%

"TO PROTECT LIVESTOCK"..... 5.6%
"NO RESPONSE".....15.6%
"OTHER".....25.2%

A combination of diverse responses comprise the "Other" category, and include, for example: "for environmental reasons" (3.3%); "political greed" (3.1%); "to protect humans and pets" (2.8%) and the like.

We took a liberty with the next question, the point of which was touched on only very slightly in yesterday's talks. It's not only important to hear what's being said, but it's also important to hear what's not being said. Many of us here today know that the basis for wolf management, or control, is not solely a biological one; and a majority of the general public perceive it for what it is: primarily an economic/political one. "Low prey density", after all is a value judgement. And, as Bill Gasaway stated so clearly yesterday, "Wildlife management need only occur when man wants something an unmanaged system does not provide."

"DO YOU SUPPORT MANIPULATING WILDLIFE FOR HUMAN ECONOMIC BENEFIT?"

"RARELY OR NEVER" 69%

When we asked,

"DO YOU AGREE WITH THE KILLING OF WOLVES TO PROVIDE MORE BIG GAME FOR THE HUNTING COMMUNITY?"

"NO" 90%

When asked,

"DO YOU AGREE THAT WOLF CONTROL PROGRAMS SHOULD CONTINUE?"

"NO" 66%

In answer to our question,

"DO YOU SUPPORT THE USE OF AERIAL WOLF CONTROL?"

"NO" 79%

In addition to the resounding "NO" given to wolf control programs in place to increase ungulate populations for hunting by OUR sampling of the general public, I would like to add some insights from a study published by the Ministry of Environment in 1987, entitled *Wolf Control in British Columbia: the Public Controversy* (R. Hoffos, 1987).

Respondents to this survey were asked if they felt that:

"MAJOR DECLINES IN SOME PROVINCIAL PREY POPULATIONS (DEER, MOOSE, ELK, CARIBOU, MOUNTAIN SHEEP) ARE DUE LARGELY TO PREDATION BY BEARS AND WOLVES"

LIVESTOCK OWNERS	HUNTERS	NON-HUNTERS
Agree 29%	Agree 32%	Agree 10%
Disagree 58%	Disagree 58%	Disagree 83%
No opinion ... 13%	No opinion ... 10%	No opinion ... 7%

Note that 58% of *both* livestock owners and hunters disagreed with this statement.

When they were asked if they felt that

"LOCAL DECLINES IN SOME PREY POPULATIONS ARE DUE LARGELY TO PREDATION BY BEARS AND WOLVES"

LIVESTOCK OWNERS	HUNTERS	NON-HUNTERS
Agree 35%	Agree 45%	Agree 20%
Disagree 55%	Disagree 43%	Disagree 65%
No opinion ... 10%	No opinion .. 12%	No opinion ... 15%

This study indicated that even a majority of those who are supposed to be the beneficiaries of wolf control, do not believe that wolves are responsible for declines in prey populations.

In summary then, general public support for wolf control as a means to increase ungulate numbers for hunting is extremely limited. In fact, based on the results of our survey, we believe that there is a substantial portion of the population who, if a public referendum on whether or not wolf control should be used to increase ungulate populations for hunting, would soundly reject the program(s).

Perhaps public insecurity about the future of B.C.'s wildlife is supported by the general awareness that wolf control programs are carried out despite very limited concrete knowledge of the consequences. The public is also aware of the liberal wolf hunting and trapping opportunities throughout this province, and of the numerous illegal killings and poisonings. Meanwhile they perceive very little effort being made towards the preservation of this species -- a species of unique character whose available range throughout North America has shrunk dramatically -- and they are concerned.

Every nation has a responsibility to humanity at large for ensuring the survival of its native wildlife. Representations have been made to us by British Columbians, including many of European origin, who fear B.C. may be following the same path of wildlife management that led to wholesale destruction of wildlands and wildlife in Europe - a program of total human manipulation. To underscore the folly of this course, in Sweden, for example, where the wolf has now been eliminated, the number of moose has risen so drastically that they are destroying crops and orchards, and causing almost 6,000 road accidents a year, despite heavy human hunting pressure.

Northwest Wildlife trusts that the wolf will not suffer a similar fate - in the long run - in B.C. Our survey , as well as over a years worth of public input, indicates that the public is becoming more concerned as it becomes more informed, and it clearly does not want the whole of the environment managed or manipulated "for the benefit of humans". To many, the bottom line is that wolves -- as an important component of wildlife -- have an unquestionable, intrinsic value that the public wants retained.

We are not suggesting that the Wildlife Branch get out of the wildlife management business. These results and others suggest, however, that the *priorities of wildlife management need to be redefined.*

Recent studies conducted by the Ministry of Environment, Wildlife Branch, reveal that B.C. residents participating in non-consumptive, wildlife related activities are already generating close to $490 million dollars per year. This, even prior to the formal implementation of wildlife viewing tourism here. These studies show, as well, that almost 88% of B.C. residents are interested in non-consumptive wildlife activities, while less than 5% of B.C. residents hold hunting licenses.

Despite the implications of these figures, it is widely known that still the majority of wildlife management decisions support the consumptive use of wildlife. Those who purchase hunting licenses seem to gain the most input into

wildlife management decisions. Would the government respond more favourably to the non-consumptive public's desires if they paid a fee to the Wildlife Branch over and above taxes? These additional funds, possible going directly to the Wildlife Branch, could allow them to carry out more often pro-active, rather than re-active, programs on behalf of wildlife, and fulfill thereby the expectations of the broad majority.

B.C. has a concerned public holding its government accountable for the province's wildlife. They perceive that the consumptive use of wildlife is the primary motivation behind wolf control programs, and they find this disturbing. Why, they ask, are the already limited resources of the Wildlife Branch not redirected towards the more important area of wildlife and wildland protection?

Then we come to the great unspoken issue, the concept of "wildlife management" itself. The consumptive interests rely on the co-operation of the Wildlife Branch for what is often referred to as wildlife "enhancement" or "control". The perceived need for "control" implies that something is out of control -- or that man has greater insight into the problem than do the forces of nature.

Man is what is out of control.

An ecological balance, disrupted at first by man, is thrown even further out of alignment by ongoing "management" -- specifically in this case, by wolf control. Dr. David Suzuki notes that once we are embarked on the use of management,

> "... we become dependent on it [management] because of the enormous ecological upset that results. ... In short, an ecological balance that is achieved and maintained over thousands of years is thrown cataclysmically out of whack."

I ask you to consider this: in our own brief lifespans, when we perceive an ungulate herd as declining, who are we to say that is not an important result of the ecological ebb and flow? Why kill off wolves to preserve a local ungulate population whose time may simply have come, or whose range may be altering? And who are we to say that it shouldn't change, and that every effort must be made to prevent it?

If the *future* of the *remaining wilderness system* in this province is to be determined *by manipulating wildlife* so completely, in order to rationalize, to industry, the retaining of that wilderness, then current wildlife management is doing nothing different from industry. We will be on the road to failure - taking wildlife with us.

Priorities must be clarified. We can stop industry's demands for wildlands only if we come together, even with our differences, to preserve wildlands for what they are. But allowing the "Catch 22" of manipulating - and thereby destroying - most of the remaining wildlife systems "for high prey densities" as a rationalization to preserve forests, is the sure road to failure - in the long run.

B.C. is fortunate, in that it still retains some wilderness areas large enough to preserve both wolves and their prey. But these pristine areas are vanishing quickly. The National Parks on our borders are under increasing pressure from year-round human visitors. B.C. must create wildlife wilderness areas where wolves and their prey can be left to carry on with their age-old interactions. Canada is one of the last remaining strongholds of the shrinking wolf rangelands in North America, and there is little guarantee it will remain so unless SPECIFIC steps are taken provincially to ensure the wolf's survival.

Government must establish wilderness areas where both wildlife -- and visitors -- are free from the impact of resource extraction. And establish wilderness where wildlife will be free from humans and their impacts.

Dollars and cents arguments are often pieced together to validate actions that are detrimental to the environment, but if I must illustrate an economic rationale for preserving the wolf here in B.C. one need look only at the success of places like Algonquin Park in Ontario. It is presently the largest wolf howling area in Canada, and a most popular and successful tourist attraction as well as educational facility. A few other areas in Canada have instituted various kinds of wolf howling programs, *but B.C. is not among them.* The concern and interest in the wolf and the developing interest in wildlife viewing tourism could prove extremely productive economically for B.C. -- especially since B.C. still retains what many other areas have lost, forever.

Public interest and concern for the wolf is growing. For many, the wolf is the symbol of true wilderness. To others, the wolf control programs are a symptom -- a symptom of man's attitude toward his environment as a whole -- an attitude which, if left unchecked, will eventually lead to the destruction of B.C.'s abundant, natural wildlife and wilderness.

There is another factor in the equation of economic definitions or scientific rationale regarding wolf control. Economics and Science are the rulers of the human heart, and the public at large is speaking from its heart. Many times in the past we have let our personal situations compromise our actions. Therein lies the future challenge, as *the environment* and the remaining life within it *can no longer afford to be compromised.*

The general public is stating that it wishes to have positive action taken on behalf of the wolf -- and all wildlife. They are depending upon those in decision-making positions to hear their desires, and then act upon them, while we here in British Columbia, unlike other countries, still have options.

I believe we are in a transitionary time. Wildlife is and has been managed primarily as a consumptive commodity. The main premise for wolf control is an additional factor illustrating man's self-defeating impact upon the natural environment. The general public is concerned about that because they -- WE -- are becoming starkly aware of the rapid destruction of so much of the world's natural environment, and the British Columbian public sees the pressure mounting in their own Backyard. mankind has had a long history of over-exploitation; and this may be the last stand that the general public - in B.C. - can take in a land where there is still a choice of options in the outcome.

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When Is Wolf Control To Increase Ungulate Numbers Justified?

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"The greatest danger to the timber wolf lies in the future - in the latter part of the century - when large areas of big-game range are no longer inaccessible, when the annual hunting kill has finally approached the production of the herds. What will our attitude be then? Will we be willing to share deer, moose and caribou with the wolves?"

The late Douglas Pimlott asked this question in 1961, in perhaps his best known article "Wolf Control in Canada" published first in Canadian Audubon Magazine. He ended that article with a prediction that the future of the wolf will not be bright unless more people come to appreciate the positive and aesthetic values of the wolves.

I am another person at this symposium who was deeply influenced by Doug Pimlott. I was fortunate to have studied wolves, and a whole lot of other things about wilderness, under him both as an undergraduate and graduate student, and later as a colleague. Much of yesterday's discussion almost assumed the logical necessity of killing wolves if they are shown to limit prey; that disappoints me because it is not the answer I would like to be hearing to Doug's question directed to the latter part of this century - now. I think it would disappoint him too.

Also bothersome were suggestions made a number of times yesterday that in the last decade biologists have shown that wolves limit ungulate numbers much more commonly than previously believed. Let me remind you that in 1967, at a major wolf symposium published in the American Zoologist, Doug Pimlott postulated that ungulate population limitation by predation in North America likely represented an evolutionary norm.

"Harvest, removal, manage, manipulate, kill, protect" - we have heard all these words espoused as appropriate human reactions to wolves in the past day and a half. Some of you are deeply committed to the legitimacy of government-sponsored wolf control, or to hunting wolves as big game, or

trapping them, or protecting them. All these relationships are reflections of the mixture of today's societal values. With such plurality, how can we find an appropriate way to manage this controversial carnivore?

Management biologists are often caught in the middle. Government employees are not always free to speak out, and that adds confusion to public debate. But they can help themselves, and the concerned public, by insisting on clear policy at the outset, and that they be allowed to assess the biological justification for any proposed killing.

Yet, even the choice of ways to seek biological justification cannot be done in absence of values. Even a scientist's or manager's very approach to conducting research is an expression of his values. If these values are not stated explicitly, they are by his actions. Few issues in wildlife management better illustrate this reality than the ways of seeking biological justification for wolf control. There is more than one method, with very different value-underpinnings. I will explain the methods, then turn to the values they represent.

One way the biological role of wolves on a prey population can be estimated with reasonable accuracy is by inductive inquiry. Among speakers at this symposium you heard examples of inductive inquiries from Francois Messier (Laverendry Park), Rick Page (Isle Royale), and Lu Carbyn (Riding Mountain National Park). An inductive inquiry involves collecting evidence that can indicate whether or not wolves are limiting the size of the prey population. I will review this evidence, but first it is worth considering the range of relationships which can exist between wolves and their prey, from which to pick the operating one in any specific case.

Picture a prey population as a buoy floating somewhat submerged in the water, held below the surface by an anchor - the wolf population (Fig. 1). The surface of the water is the maximum height the buoy can reach - the 'nutrient/climate ceiling' or the 'carrying capacity' set by available food. The connection between buoy and anchor is elastic, not a chain, so the two can be at different distances from one another, that is, the predator:prey ratio can vary.

In Fig.1 Model A, the wolf population is limiting the size of the prey population. If the anchor was removed, the buoy would float up to the surface - the nutrient/climate ceiling. This situation is described in seven out of 18 studies in which data are sufficient to draw conclusions about ungulate population limitation with wolves present, reviewed by Connolly (1978) and

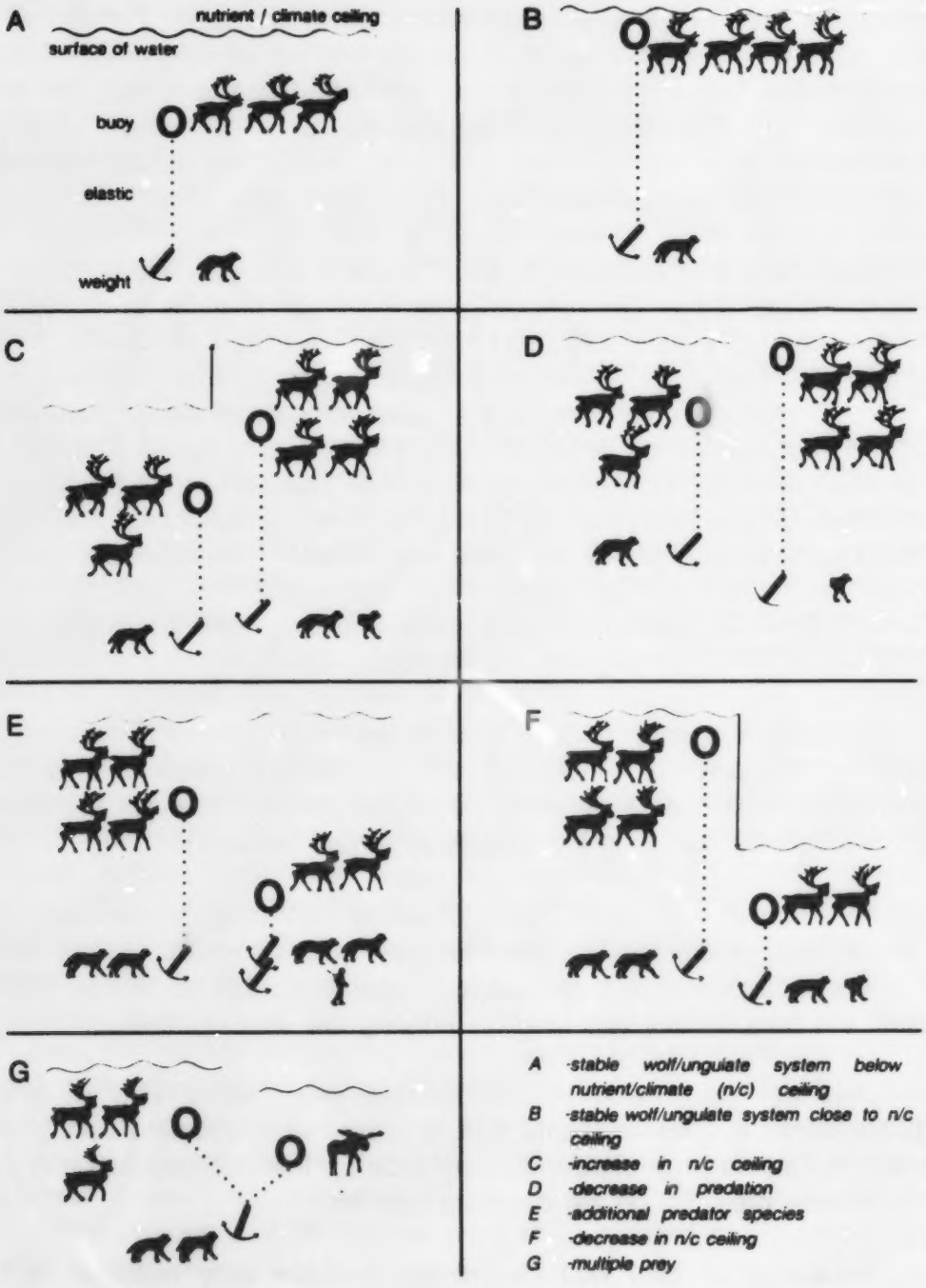

Fig. 1. Models of wolf/ungulate relations

Theberge and Gauthier (1985). (The latter reference goes into more detail on the models which are reviewed here.)

In Model B, the buoy is at the surface. Cutting off the anchor would not increase the size of the prey population. Mortality caused by wolves here is called 'compensatory', that is, if wolves do not kill them, starvation will. This situation occurs when the size of the wolf population is limited by something other than food availability, such as disease, or in a multiple prey situation where wolves feed to a large extent on something else. Multiple prey complicate the picture and will be addressed again later.

Also more complex is a situation where the height of the nutrient/climate ceiling goes up (Model C). Despite seeming control on the prey population by wolves on the left side of the diagram, if the nutrient/climate ceiling goes up, so may the prey population. This situation is described in a number of ungulate eruptions. I am currently investigating what appears to be an example of this model in Algonquin Park where spruce budworm and logging appear to have raised the nutrient/climate ceiling. The moose population has responded rather dramatically despite the presence of a healthy wolf population. This model also portrays the 'habitat improvement' option to increase ungulate numbers.

In Model D, starting out with wolves limiting their prey (Model A), wolf control creates a larger prey population (Model B).

In Model E, human hunting adds to the kill by wolves to depress the prey population. Co-predator - man and wolf - cause this decline in prey, especially if wolves have no alternative prey species to turn to. The ability and speed of prey switching by wolves is the subject of current research.

In Model F, the nutrient/climate ceiling has dropped, perhaps due to a series of harsh winters. The predator:prey ratio increases - more wolves per prey - and wolf predation is termed 'anti-regulatory', that is, wolves steepen and deepen the prey decline and possibly prolong low prey numbers.

One last relationship depicts multiple prey (Model G). If one of the ungulate buoys is lowered, either due to lower nutrient/climate ceiling or human overkill, the stable prey population may prop up the wolf population and allow it to exert more pressure on the declining species.

Reviewing all this, wolf control will increase prey numbers in Model A (shown in Model D), Model E, and Model G depending upon the proximity of

the ungulates to the nutrient/climate ceiling. It will not increase numbers in the others.

Fig. 2 shows some of these same relationships between wolves and their prey in a different form, with "ungulate density" on the Y axis and "time" on the X axis. The sequence of relationships in this figure portrays a realistic variation that may occur in some sequence or another over time, because wolf - prey relationships are dynamic. The initial relationship is the same as Model A, with predation limiting the size of the ungulate population. Then, with increased human overhunting, the prey may decline as in Model E, resulting in less prey per wolf and invoking 'anti-regulation' such as described for Model F, sinking the prey in the 'predator pit'. The prey population may escape from the pit following prey switching, and/or reduction in predator numbers (Model D), and/or an increase in the height of the nutrient/climate ceiling (Model B). This figure and a more extended discussion of it is found in Gauthier and Theberge (1987).

The literature on wolf - prey relationships indicates this range of relationships. How do you determine which one is operating? By answering a series of questions (Fig. 3). Essentially, these questions address alternative explanations for ungulate population limitation: Is the population up against its nutrient/climate ceiling (Model B and F), or has emigration lowered numbers, or is human kill adding heavily to the loss of ungulates (Model E) or is another predator species exerting significant impact? These questions are discussed in more detail in Theberge and Gauthier (1985).

Techniques exist for answering all of these questions. They may take two or three years to answer and a budget that will vary with accessibility and pre-existing information. There are not any reliable shortcuts. Specific predator:prey ratios, sometimes suggested as indicators, mean nothing by themselves. You have to know the relationship of the species to the nutrient/climate ceiling, and in a multiple prey situation, the proportion of different species in the diet.

Two recent studies with which I have been involved have allowed us to assess the most appropriate model. The first study, in the early 1980's, formed the PhD research of Dr. Dave Gauthier, now on the faculty of the University of Regina. About 400 caribou, the Burwash herd, occupied two tundra plateaus in the southwest Yukon. Approximately 10-14 wolves in two packs hunted these caribou. Three wolves, and 36 caribou were radio-collared in the course of the study. Key findings were:

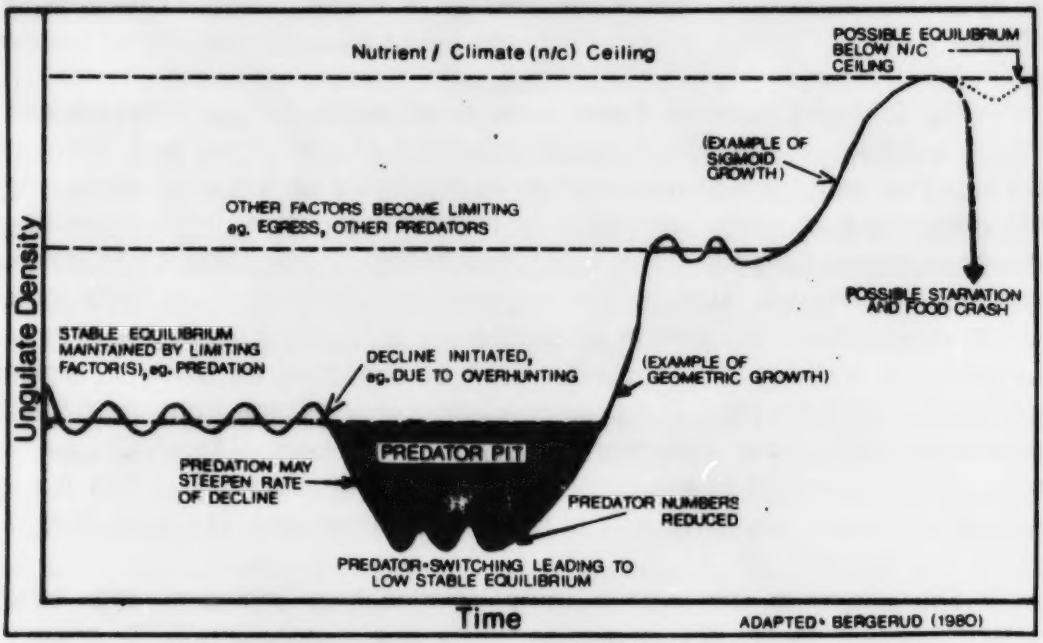
Nutrient / Climate (n/c) Ceiling
POSSIBLE EQUILIBRIUM BELOW N/C CEILING
(EXAMPLE OF SIGMOID GROWTH)
OTHER FACTORS BECOME LIMITING eg. EGRESS, OTHER PREDATORS
POSSIBLE STARVATION AND FOOD CRASH
Ungulate Density
STABLE EQUILIBRIUM MAINTAINED BY LIMITING FACTOR(S), eg. PREDATION
DECLINE INITIATED, eg. DUE TO OVERHUNTING
(EXAMPLE OF GEOMETRIC GROWTH)
PREDATOR PIT
PREDATION MAY STEEPEN RATE OF DECLINE
PREDATOR NUMBERS REDUCED
PREDATOR-SWITCHING LEADING TO LOW STABLE EQUILIBRIUM
Time
ADAPTED: BERGERUD (1980)

Fig. 2 General concepts about wolf ungulate relationships. Examples of both geometric and sigmoidal growth of an ungulate population are shown. Either of these growth forms could lead to the nutrient-climate ceiling. The stability shown at the top of the geometric curve is not necessary but represents that either growth curve could be halted before reaching the nutrient-climate ceiling.

1. Do population censuses show the ungulate population is increasing?
   - → YES. No control.
   - ↓ NO

2. Do habitat analyses show relatively poor seasonal forage availability and/or quality, and does assessment of physical condition indicate that a relatively substantial proportion of animals are suffering from malnutrition (kidney fat, body weight, etc.) and/or diseases (blood and tissue samples)?
   - → YES. No control.
   - ↓ NO

3. Are climate indices for winter and calving periods correlated with ungulate population mortality rates?
   - → YES. No control.
   - ↓ NO
     - → If population is stable, predation is probably limiting. Go to question 5.
     - → If population is declining, go to question 4.

4. In a declining population, does egress substantially exceed ingress to the population?
   - → YES. No control.
   - ↓ NO

   Predation probably limiting. Go to question 5.

5. a) Is major cause of calf and/or adult mortality (both should be examined) wolf predation as determined by mortality collars or sightings of kills?

   OR

   b) Do wolf numbers and food habits (latter determined by scat analysis and/or finding sufficient kills) indicate that the number of the ungulate species killed is significant relative to productivity?
   - → YES. Wolf control may increase prey numbers[1,2]
   - ↓ NO

6. Percent kill by hunters is of significant size or has increased.
   - → YES. Reduction of human kill may be necessary.
   - ↓ NO. Other predators are significant.

[1] Killing wolves in a multiple predator situation may not produce more ungulates if compensatory increase in predation by another predator species occurs

[2] Despite the conclusion drawn here, one should assess question 6 in order to understand the proportional effects of wolves and humans.

Fig. 3. Systematic set of questions to determine if wolves are limiting their ungulate prey.

1. The caribou population was relatively stable over the four years of study.

2. Caribou made up 35% of the total biomass of food, moose 30%, and snowshoe hare near the peak of their cycle 21%.

3. Annual caribou mortality was about what you would expect in a stable population, or slightly lower - 6 to 9%.

4. Wolf predation accounted for more than 60% of all caribou deaths, including neonates. About 25% of neonates were predated.

5. Caribou were not at a nutrient/climate ceiling. Lichen availability was assessed on transects, as was snow patterns that may have made lichens unavailable. There was plenty of available food. Also, caribou that were handled were all in good condition.

6. Human kill accounted for 7-13% of the annual mortality, so was a much less significant influence on caribou numbers than were wolves.

7. Severe spring climate conditions killed neonates heavily in one year, and grizzly predation was implicated in one year. Nevertheless, Model A appeared to be appropriate here, as far as caribou were concerned, that is, the size of the caribou herd appeared to be limited by wolf predation, although the degree of potential compensation between wolf, grizzly, and man was unknown. Details of this research are in Gauthier (1984) and Gauthier and Theberge (1986).

A very different environment in southcentral Labrador is the home of the Redwine Mountains caribou herd studied for an MSc degree by Kent Brown, now a wildlife consultant in Calgary. About 700-800 caribou lived here, most of the time scattered across 25,000 square kilometres of flat open boreal forest. The population over the two years of study was stable or declining slightly.

Snow is deep here, often up to two metres, so this herd contends with the deepest snow of any herd in North America. They do so by cratering, and eating arboreal lichens, until late winter when a sun-crust on the snow appears

to make travel even more difficult. Then, many caribou migrate to the rolling tundra Redwine Mountains themselves, really a rolling plateau of about 160 square kilometres. For about two to three weeks in May these concentrated caribou are set-up for predation. Much of their mortality occurs then, 2/3 of which was caused by wolves and 1/3 by black bears recently emerged from hibernation. So, while predation was the most important proximate cause of mortality, snow conditions, which caused the caribou to concentrate, was a predisposing factor.

Caribou were suffering a protein deficiency in late winter, shown by very low blood urea nitrogen, the lowest we could find in the literature. While they were not dying from it, they may have been weakened, facilitating their capture by predators.

We concluded that here was a Model B, with the herd near a nutrient/climate ceiling. Wolf control may have done little or nothing to caribou numbers. This research is described in Brown's thesis (1986).

There is another equally valid, perhaps even more valid scientific approach - a deductive or experimental one. Kill wolves and see what happens. If prey populations go up, wolves were limiting them; if prey do not go up, wolves were not. (While this approach seems more straightforward than an inductive inquiry, it too has uncertainties. Variables such as weather, disease, size of alternate prey populations, and other extrinsic factors may not be constant on a control and removal plot, two large areas of wilderness.)

Here we come to the interface between science and values. The deductive, experimental approach accords no worth whatsoever to the wolf. It works from the premise that no harm, no injustice, no malpractice is done if a bunch of wolves is killed unnecessarily. We kill mosquitoes, cockroaches, ants without moral misgivings or fear of social reprisal, but we don't kill other humans, whooping cranes or California condors.

The predictable public controversy that surrounds wolf control clearly shows that wolves are no longer in the cockroach category. It seems clear that a large segment of the public will not accept wolf killing before the biological case is made. Yet, we have governments that still apply cockroach policies. Some biologists, by their actions, do likewise.

But a much bigger issue of values is whether wolf killing, even when it may increase ungulate numbers, is unacceptable. Quite possibly the majority of

Canadians see it that way now, on the same ethical grounds that govern attitudes towards the killing of harp seals, the trade in endangered species, and commercial whaling. Conservation groups, in the interests of seeming "rational", may even lag, not lead, public opinion on this issue. Governments which announce wolf control invariably receive floods of mail from people who simply object, regardless of the biological situation.

Are these people to be ignored - called 'condominium conservationists', or are they to be thought of as possibly in the vanguard of a new emerging ethic? Ethics in society change. Once slavery was in vogue. Doing away with slavery caused considerable economic and social hardship. A lot of social reform has been brought about by changes in ethics. Is it unreasonable to expect changes in ethics to lead to environmental reform?

Well, back to Doug Pimlott. We had many fine adventures together with wolves in Algonquin Park. Doug died a slow death from cancer. And during that time he planned his memorial service, the one at which he asked Monte Hummel to preside. Doug wanted even his death to serve some purpose, to be inspirational. He phoned me near the end and asked that his memorial service end with a wolf recording that I was to select from my collection, many of which we recorded together. "Not a melancholy one," he said, "but one that is upbeat with pups in it."

That recording, when it resounded in the chapel at the University of Toronto, was a moment that none present will ever forget. We have all had a different set of experienced that has led us to view wolves however we do. Because of a particular play of events in my life, and my experiences with wild wolves, I have come to see the wolf as an essential part of large mammal systems, wild and free, which form the essence of wilderness in Canada. Despite my training as a wildlife biologist, wolf killing to increase ungulates no longer fits.

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WILDLIFE MANAGEMENT IN BRITISH COLUMBIA

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First, I would like to thank the organizers of this symposium for the opportunity to come here and learn more about wolves from this impressive collection of experts and secondly, for generating a debate on this subject in a forum other than the Vancouver Sun or the Los Angeles Times. This is an issue that has generated much heat over the past ten years and hopefully this symposium will help to throw a little light as well.

I am not naive enough to think that one symposium will lay to rest all the controversy which this issue has generated over the years. Both sides are pretty well dug into fixed positions and old tapes continue to be played every time one mentions wolf control. One information exchange will not change that, but it is definitely a beginning.

Nor will I attempt to go farther down the technical road and talk about individual projects. The speakers ahead of me all know much more than I about wolf biology, population dynamics, program design, the vagaries of statistics and the conclusiveness of the results. What I can give you is my perspective as program director about where predator control fits into our overall management scheme for the Wildlife Program in B.C.. As such, I have a delicate task. The strength of this symposium is that for the first time in this province, people are debating the technical and biological factors of wolf control in a scientific atmosphere and that is an approach that I do not want to jeopardize by highlighting the even more controversial social and public relations aspects.

But let's face facts. There is almost no such thing anymore in wildlife management as a purely technical issue and managers cannot simply fall back on science as the sole rationale they need in order to proceed with a program. Some good scientific programs may be morally, ethically, or socially unacceptable and all these factors need to be considered when making a management decision about wildlife. The long-term survival of wildlife on this planet is an emotional issue and it will continue so.

What I want to do is explore with you some of the aspects of wolf control as it affects wildlife management and hopefully give you some idea about the philosophical direction we are coming from. You need not agree with me, but I want you to have some appreciation about the thought that underlies wildlife management in B.C.

In most of North America, the management of wildlife has two faces. On one hand the preservation and protection of wildlife to ensure that they will be around for the future, is a principle that almost every one agrees with. Some people and some jurisdictions may not give it the priority we all would like, but most people agree that there should be no compromises if we are talking about the long-term survival of wildlife populations. But when we come to the short-term *use* of wildlife and by "use" I include aspects such as viewing, or simply appreciating wildlife, not just hunting, the sentiments of the public diverge from those of the managers. People disagree about how far we should go and what we should practice under the umbrella of wildlife management. This dilemma is created by the fact that much of wildlife management is really more of an option than a necessity. Let me illustrate this as follows. In the Ministry of Health, there are some programs that we may disagree with, but we would probably all have to grudgingly admit that they are necessary. You may philosophically disagree with the testing for certain diseases, but the government may decide to do it for your protection in spite of you. In a similar vein, the Ministry of Transportation and Highways has to build roads to a certain standard for your safety, whether you appreciate their using your tax dollars that way or not.

In the practice of wildlife management, we are not faced with such readily obvious absolutes and the correct ethical or moral and even sometimes, the scientific path, is more difficult to find. We are essentially doing what *you want* when it comes to wildlife management. If enough people in this province want recreational hunting, such hunting will continue. If no one wants falcons captured, there will probably not be any captures in future. Such policy direction, based on the will of the majority, is the basis of the system.

The Wildlife Program thus has to listen to all the conflicting messages and determine which is the correct route to follow in managing the wildlife resource for the people of this province and on the larger scale, fulfilling its international obligation as the protector of some unique species on behalf of the whole world. We have an obligation to come up with the sort of wildlife management program that will satisfy most of the people in this province.

In pursuit of this proper management direction, the Wildlife Program is based on the following overall goal:

> To manage the wildlife resource of B.C. for the benefit and enjoyment of the people of the province, by maintaining the optimal balance between ecological, cultural, economic and recreational needs.

Under that goal, the most important objective is as follows:

> To maintain and enhance wildlife and their habitats to ensure an abundant, diverse and self-sustaining wildlife resource throughout the province.

And after that prime directive, the other four objectives are as follows:

> To maintain, enhance, and promote opportunities to appreciate, study and view wildlife in their habitats.
>
> To maintain, enhance and promote recreational opportunities to hunt game species in their habitat.
>
> To facilitate the commercial use of wildlife.
>
> To protect people and property from unacceptable levels of danger or damage from wildlife.

Those are the directives which drive the Wildlife Program but there are other principles that fall out from these goals. One of the main ones is that all our programs and our efforts are predicated on *maintaining the health of ecosystems on which animals depend, not on the welfare of individual animals.* And it is here that we diverge most radically from the views of the public, who have been inundated with the cult of the "individual animal" from American T.V.

Our main efforts are spent in attempting to influence the activities of the forest industry, the agricultural industry, the mining industry, etc., so that we can maintain the habitats and conditions necessary to keep animal populations around for years to come. Since we have limited staff resources, we tend to concentrate on this to the exclusion of individual animal welfare. We are in this wildlife management game for the marathon, not the sprint and we are dedicated to ensuring that the systems that support wildlife are intact 50 years

from now. We think the real test of the success of the Wildlife Program is not whether we satisfy every user group *now*, but whether we have enough wildlife around in 50 years, so that the debate about use is still relevant. If we have a choice between spending $2000 to move an offending bear from the Lower Mainland or sending someone on a site inspection of a logging block that, if preserved, will continue to support ten bears for the next 100 years, we will probably shoot the offending bear and spend the money on the logging plan. Harsh words, but realistic ones in these days of limited budget.

Basically, then, we made a decision long ago that we would concentrate our efforts on the preservation of systems that support wildlife. What follows from this is that *as long as the system is healthy, we will promote ethical uses of wildlife within those systems as long as those uses do not jeopardize the long-term health and survival of the populations.* And similarly, *we will implement short-term measures to manipulate the strength of various populations as long as the basic productivity is not put into question - hence predator control.*

I believe that if the forces in this province who oppose wolf control were successful right now in stopping any more wolf control programs, it would have a negligible effect on the question of the long-term survival of the wolf in this province. The future of the wolf will be decided in large measure by the extent of future logging activity, human settlement, agricultural expansion and increased unregulated access.

So if those well meaning people who want to see wolf control halted are successful, I think the results should be put in perspective.

You may have made an ethical point about the use of wildlife and the philosophy of interfering with nature and it may be important and enough for your group that you do this, but you will have done little to save the wolf in this province. That fight will be won or lost by hard negotiations in government and in the boardrooms of industry. If you really want to help the wolf, don't parachute into the Muskwa and confront John Elliott; parachute into some of the current land use debates in this province and confront those who would use the land irresponsibly.

One hundred and twenty years ago on this continent there were the beginnings of what we could call "environmental protest" groups, who were opposed to the wholesale killing of buffalo. Had these groups been successful in halting the commercial slaughter of buffalo when there were still 20 million left, would they deserve our thanks today and what would they have accomplished? I suggest

to you it probably wouldn't have mattered, because what ultimately doomed the great herds of buffalo was the conversion of the American Plains to intensive agriculture. That same sort of scenario is still at work today and if you don't take anything else away from my few words, I want you to realize that the increased price for wood, minerals and agricultural products have the real potential to do what John Elliott's shotgun will never do. If you believe that, I urge you to assist us in supporting the type of land use planning and land use decision making that will shape this province and its wildlife resource in the future. If you do not, perhaps you should go back to watching Marty Stoeffer's "Wild America".

We recognize the controversy that is created by predator control problems and there is no way around that debate. There will be even more controversy about wildlife in the years ahead in this province as development, human settlement and agriculture expand and wildlife and human enterprise come more in contact. We will see heated debate about agricultural damage caused by wildlife, about the need to destroy problem wildlife in urban areas, and the desirability of continuing recreational hunting. We know that the major predators will receive more and more attention by the press and the public. For this reason we have embarked on major reviews of the status in this province of grizzly bears, black bears, cougar and lynx so we can apply the right management scenarios to them. If there is any question about their populations, there will be no hunting or extremely restricted hunting. That has always been a cornerstone of the Wildlife Program and we apply the same sort of rigorous scrutiny to all the predator control programs as well.

One of the complicating factors in the predator control equation is, of course, who benefits from the control? Critics say that a main benefit is to the recreational hunter and this is to a large extent true. The Wildlife Program is not ashamed of recreational hunting. If we were, we should stop doing it. But we are not, and we do not intend to continually apologize for it. I believe much of the public criticism of wolf control is based on the fact that some groups do not want to see hunters benefit. As far as we are concerned, recreational hunting is a valid use of the wildlife resource and one that is sanctioned by government and in legislation that was passed by government. As such, we believe that management techniques such as predator control are justified to meet our objectives and to keep some populations at a level that allows them to be exploited by man.

And yes, we do want more wildlife around in many areas. More wildlife means more users and more tourists and that means that when a land use decision is to be made about an area, we are able to put forward a case that, if the area

is left intact, the wildlife resource will be able to generate significant economic benefit on its own. And in the cold hard light of day, economic arguments are usually the ones on which such decisions rise and fall.

You may not like our emphasis on economic argument and you may think that quotes such as "saving our heritage for our children" or "travelling together on the Spaceship Earth" can be just as effective as the economic approach to a politician. If you believe that, I would like to talk to you later about some recreational land I have for sale in Florida.

Seriously, there is value in being able to make a long-term case for wildlife, based on potential to generate return and that argument is more defensible when healthy numbers of wildlife are present.

There is an interesting predator situation developing in the Queen Charlotte Islands. Initial studies confirm that raccoons and rats are depleting populations of auklets and murrelets. These seabirds are the main food source of the Peale's Peregrine Falcon. There is a very real danger that if we do nothing to control the predators, the population of seabirds will go down and supposedly the peregrines will follow. They probably won't go down to extinction, but it is probable that there will be less seabirds and hence less peregrines.

No one hunts these seabirds, they are totally protected. So any control will not benefit hunters. It will benefit naturalists, who like to view these large seabird colonies and supposedly birders, falconers and naturalists who also like the falcons. What is the criterion to be used in making a decision to control the Queen Charlotte raccoons? Is it who benefits, i.e., is one group more deserving than another? Is it how far down the prey population is likely to be driven? Is it the world class profile of the falcons that will likely benefit? Or should we leave them alone?

No one knows yet what will happen in the Charlottes and what the management decision will be. We need more information, but this issue should give some pause to those who see the wolf control issue as simply black and white. I expect if some control is instituted in the Charlottes, that the next week the Minister will get a flood of letters from the "Friends of the Raccoon", stating that all we ever think about is satisfying the naturalists!

There are many ways the whole debate about predator control can be improved in this province. One of these is for the Wildlife Branch to take more seriously its obligation to ensure that reports are made available to the public and to

disseminate information on which people can base their opinion and to sponsor and co-sponsor forums such as these where technical issues can be aired. We realize that we need to make more use of the academics and recognized wolf experts in the evaluation of our controversial programs. We haven't really done that good a job in the past and we are committed to improving this. We have an obligation to see that the information on which our decisions are based is made available to both the other professionals in the field and to the interested public.

There are also obligations on the other side of this debate and I want to illustrate it to you in this fashion. There are essentially two different points of view represented in this room. On one side are the government biologists and hunters and on the other side are the animal rights groups. Everyone in this room can be classified under those two headings. Now before you react, I want to tell you why I used the word "animal rights". I know if I use that word, I can simplify a subject that really is not simple and *more importantly*, the press will pick it up. The name *Animal Rights* sells more papers than "wildlife organization", "environmental group" or "concerned citizens". And that makes it easy to lump everyone on that side of the debate as a radical. Of course it is unfair and I know there are a great many people who are trying to see both sides of this issue and who do not deserve, or want to be put into either group. But it is no more unfair than to have the wolf control programs in this province labelled as "extermination". That is also an untruth that demeans the speaker and misleads the gullible members of the public. But like the phrase "animal rights", *it gets the attention of the press.* Let's not use euphemisms. We are controlling wolves and that means we are killing a certain number of them to reduce their effect on other species and ultimately benefit various user groups. If you disagree with this morally, ethically, socially, then say so, you have a right to make your point of view known. But base your opinion and what you tell other people on the type of technical information you have heard at this symposium, not on the more facile and sensational statement that we are exterminating wolves or the outright drivel broadcast all across Canada that there were only 55 wolves left in the Muskwa area.

We are committed to improving our decisions and technical approach to predator control, until we can hopefully satisfy many of the critics. Hopefully, we can also improve our public relations capacity, so that the citizens of this province are aware of the technical and management factors inherent in our decisions. We are always open to constructive criticism, but we want to be criticized on what we are really doing, not what you imagine or what you are fed from questionable sources.

We are not going to leave here and simply continue wolf control. We have never done that. We will analyse where we are with each program. We will digest the results of this symposium and assess how it should influence our decisions. I urge each of you to do likewise. Look at the technical information. What are the gaps? What are the assumptions? Based on this sort of review, we will make a management decision that we think is best for the wildlife of this province. We are not wedded to any one program, but we are wedded to finding the correct management direction in an issue where for every incontrovertible fact, there are a hundred conflicting opinions.

WOLF MANAGEMENT IN BRITISH COLUMBIA

W.R. Archibald
Ministry of Environment, Wildlife Branch
Victoria, B.C.

The purpose of this paper is to review the history of wolf management in B.C., outline the current wolf management strategy then provide a proposed blueprint for wolf management for the future.

Historical Perspective

Wolves were originally viewed as vermin in B.C. and elsewhere in Canada. Shortly after the turn of the century, a bounty was placed on wolves that stayed in place until 1955.

It appears that wolf numbers increased throughout central B.C. from the late 20's to the mid 40's, presumably as a result of an increase in moose distribution through the same area. These wolf increases were a major concern to guides, hunters and ranchers. In 1947 the Predator Control Branch was formed and given the mandate to reduce the number of predators damaging livestock and competing with man for ungulates.

During the 50's wolves were persecuted throughout the province. This persecution resulted in the near extirpation of wolves from the northern and interior agricultural management zones. There is little doubt that this activity also had a profound impact on the wolves in wilderness areas.

After the intense persecution of the 50's, the Ministry of Environment took a number of steps to replenish numbers in wilderness areas.

1961 - poisoning programs ceased in wilderness areas.
1963 - Predator Control Branch disbanded.
1966 - trapping disallowed.
- wolf designed big game. Hunting seasons were closed in areas of low wolf numbers. Bag limits were established.
1975 - poisons under strict control. Control of problem wolves became reactive, targeted at specific animals.
1976 - wolf designed as furbearer. Seasons established in areas with harvestable numbers.

As a result of the management action taken by the Ministry in the 60's and 70's wolf numbers in B.C. have recovered. Indeed, in some parts of the province, wolf numbers may currently exceed historic highs because of high prey numbers.

The Ministry currently estimates that there are 8,000 ± 16% wolves in B.C. (late winter estimate). This compares with a 1979 estimate of 6,300 ± 60%. This more precise current estimate is a reflection of improved inventory methods. Data used to generate this estimate include late winter aerial counts, public sightings, livestock damage reports, kill remains, scat transects, and harvest data.

Although the variances of these estimates overlap, the Ministry feels that there has been an increase in the abundance of wolves in B.C. during the past 10 years. This opinion is supported by local increases in wolf abundance and also by recent range extensions.

The most dramatic increase in wolves occurred on Vancouver Island. Between 1970 and 1972 branch staff were involved in discussions on listing the Vancouver Island wolf as endangered (Ray Halladay, pers. comm. Deputy Director, Wildlife Branch). By 1979 wolves were having a major impact on Black-tailed deer on northern Vancouver Island (Hebert et. al. 1982; Hatter 1984; Jones and Mason 1983), and by 1981 wolves were affecting numbers of deer on the southern Island (Janz and Hatter 1986).

There has been a gradual range extension in the southern interior, based on recent sightings in the Okanagan and Manning Park. This suggests the potential for recovery south of the border in the Cascades by natural dispersal.

Perhaps the best known recent range extension in B.C. has occurred in the east Kootenays. For the past 10 years wolves have been increasing their distribution southward along the Rocky mountain trench. Many of these Management Units now have manageable numbers of wolves and are being opened for hunting and trapping for the first time in 20 years.

A group of wolves inhabiting management Unit 4-1, located in the southeast corner of B.C., have moved south of the border. For the first time in 50 years there is now a breeding population of wolves in Montana state. This pack of wolves, known locally as the Magic Pack, has come to exemplify the struggle between supporters and opposers of the wolf. In both jurisdictions the management agencies are caught in the cross-fire. I will expand on the social aspects of wolf management later.

Current Management of Wolves in B.C.

The stated management objectives for wolves in B.C. are as follows (Fish and Wildlife Branch 1979):

1. To maintain viable populations of wolves in wilderness areas.
2. To provide opportunities for people to listen to and observe wolves in their natural habitat.
3. To control wolves in established livestock management areas.
4. To control wolves on a site specific basis where the main objective is to maintain another wildlife species at a desired level.
5. To provide for the hunting and trapping use of wolves.

Following is an evaluation on Branch activities related to each of these management objectives.

1. To maintain viable populations of wolves in wilderness areas.

   As mentioned previously wolf numbers throughout the province appear to be increasing. The long-term viability of wolves in wilderness areas seems to be secure.

2. To provide opportunities for people to listen to and observe wolves in their natural habitat.

   Although opportunities exist for the public to observe and listen to wolves in most areas of the province, the Branch has not yet actively promoted this activity. However, the Ministry has recently revised the objectives of the Wildlife Program and one of the revised objectives is to promote the viewing of wildlife. In conjunction with this new objective the Wildlife Branch has entered into a partnership with the Ministry of Tourism and has identified over 300 sites that have viewing potential. Some of these sites are wolf viewing and listening sites.

3. To control wolves in established livestock management areas.

   The existing policy governing the control of problem predators was implemented in 1979. This policy was developed with the assistance of the Problem Wildlife Committees, which consist of representatives from the Ministries of Agriculture and Fisheries and Environment and Parks, and livestock producer and conservationist organizations within the province (Tompa 1983). This policy states that wolves can only be controlled on a site specific basis where

there are verified attacks on, or harassment of, domestic animals or threats to human safety. This policy requires that wherever possible conflicts with livestock be resolved through improved husbandry practices and that control be directed at individual wolves and packs causing a local problem.

Since 1976 there has been an average of 126 wolves killed annually for livestock protection. This is a maximum estimate.

4. To control wolves on a site specific basis where the main objective is to maintain another wildlife species at a desired level.

Since fiscal 1983/84 the Ministry has been engaged in 3 operational wolf control programs. These programs are located in northeastern B.C. (Muskwa), Vancouver Island and east-central B.C. (Quesnel Highlands). The total percentage of the occupied wolf range that has been subject to control since 1983/84 has ranged between 0.8% and 2.4%. An average of 126 wolves have been removed annually through Ministry Control since 1983/84 (see Table 1).

5. To provide for the hunting and trapping use of wolves.

As mentioned earlier, wolves and classified as both big game and furbearer in B.C. As big game, seasons are set and bag limits established for each Region. Current management prescriptions range from no open season in Management Units where wolves are not present in manageable numbers, to a bag limit of 10 with no closed season in areas with chronic wolf depredation problems.

Wolf trapping is permitted in Management Units with harvestable numbers. Seasons coincide with the period of pelt primeness. There is no bag limit for trappers.

Hunters and trappers have killed an average of 702 wolves annually over the last 11 years (Table 2).

Summary of Current Management

Over the past 11 years there has been an average of 907 (range 609 to 1,381) wolves killed annually by hunting, trapping and control activity. In addition there has been an illegal harvest of wolves in some parts of the province where those with a vested interest in wolf prey have been dissatisfied with the current wolf management program. It is impossible to estimate the

TABLE 1. Total number of wolves killed under Ministry control programs since 1983/84

Program	1983/84	1984/85	1985/86	1986/87	1987/88	TOTAL
Muskwa	182	198	0	125	11	516
Vancouver Island				55	50*	105
Quesnel				5	7	12
TOTALS	182	198	0	185	68	633

* estimated number

TABLE 2. Number of wolves killed by hunters and trappers

Year	Trapper	Resident Hunter	Non-resident Hunter	TOTAL
1976	151	655		806
1977	443	144		587
1978	406	479		885
1979	268	421		689
1980	228	372		600
1981	194	173	32	399
1982	186	281	40	505
1983	186	721	20	927
1984	232	577	24	833
1985	156	450	36	642
1986	201	598	45	844
TOTALS	2,649	4,871	197	7,717

illegal kill. However, despite this unknown level of illegal kill and the reported legal harvest and control activity, there has been an increase in the provincial distribution and abundance of wolves.

It appears, then, that with few exceptions, the wolf management objectives, established in 1979, are being achieved. Despite the success of this program it still remains the most controversial of the Ministry's Wildlife Program. Clearly, this program is not fully addressing the expectations of the public.

The Future for Wolf Management in B.C.

As Wildlife Managers, we in the Wildlife Branch have to be sensitive to the needs of society, particularly to the residents of B.C.

Until the late 1960's the public of B.C. were either supportive or indifferent to wolf control (Hoffos 1987). However, there now are many conflicting forces with an interest in wolf management in B.C. There are ranchers who expect protection from wolf depredations on their livestock. There are hunters who wish to pursue their activity with a reasonable chance of success and there are guide-outfitters who wish to see their capital investment protected. There are trappers who derive economic benefit from wolf trapping. As well, there are native sustenance hunters who suffer greatly when prey numbers are maintained at low levels by wolves.

To balance those groups who see wolf control as necessary from time to time are a host of groups that believe that wolf control is unacceptable. These groups have become increasingly active in the past few years and have had a significant impact on the activities of the Wildlife Branch.

Both groups mentioned above have their radical element, that is, those that would like to see all wolves killed and those that want complete protection for every wolf that inhabits the province. Both view points are economically and ecologically impractical. The challenge then is to define a management program that will satisfy the vast majority.

Research has shown that wolf control for agricultural purposes is acceptable to most (Hoffos 1987) as long as the method chosen is humane and does not pose a threat to non-target species (Arthur et. al. 1977). The public controversy appears to focus on the issue of wolf control for wildlife management purposes. Indeed, Hoffos (1987) reported that non-hunters viewed

such control programs as a threat to the long term existence of wolves in B.C. and unacceptable to non-hunters. Presumably, if the long term existence of wolves were secure in B.C., periodic, limited control activity would be more acceptable to the non-hunting public.

As well, part of the controversy surrounding wolf control relates to a lack of public understanding of the biology of wolf/prey dynamics. Much of the public's understanding of predation reflects that of professional biologists in the late 1960's and early 1970's, that is that predation is not a major limiting factor. Until the public understand the technical basis for wolf control, public resistance to any control activities will remain high.

The proposed wolf management strategy that I am going to present today has been discussed within the Ministry for the past 9 months. The principles of this strategy have been agreed upon. Details are still to be worked out.

The purpose of introducing this strategy now is to provide the public with a vision of the future for wolf management in B.C.

Wolves will be managed provincially on a zone concept. Each zone will be mapped, and will have specific management objectives, policies and procedures. In some cases, existing policies will be used. In other cases, new policies will be required.

There will be 3 wolf management zones in B.C.; population management zones, control zones and preservation zones. Each of these zones are described below.

Population Management Zone

This zone encompasses the largest area of the province. It is characterized by high wildlife demand by consumptive and non-consumptive users. This zone has a wide range of wolf and ungulate densities.

Objectives:

1. To establish a predator/prey management framework that ensures the long-term viability of both.
2. To provide recreation opportunities to satisfy consumptive and non-consumptive requirements for wolves and ungulates.

Management Principles:

1. Wolves may be harvested using traditional means, hunting and trapping, under regulated seasons throughout the zone.
2. Ungulates will be managed under a host of management regimes within this zone, depending on specific management objectives.
3. Depredation by wolves on domestic livestock will be handled according to the problem wildlife management policy.

Implications:

1. Areas within this zone may be identified for inclusion in other zones.

Time Frame:

Indefinite

Implementation:

On-going

Control Zone

These are primarily areas of highest ungulate density, or capability, which have high user demand. Generally they are small units which exist within the Population Management Zone.

Objectives:

Control zones may be established to achieve any of the following objectives.

1. To protect wildlife populations threatened with local extirpation from wolf predation.
2. To produce ungulates to meet management objectives (ie., hunting and non-hunting use, transplants, etc.)
3. For research purposes.

Implications:

1. Wolf control may require long-term financial commitments.
2. Public acceptance of wolf control will depend on a well-informed public.

Process:

Because of the need to ensure that any control program undertaken by the Branch is technically sound and, because of the controversial nature of wolf control, all proposed and ongoing control programs will be subject to the following process.

1. A review committee will be established consisting of senior Branch staff and other invited experts, as required.
2. The review committee must recommend to the Director whether a control program should proceed or in the case of on-going programs, continue. On-going programs must be reviewed annually.

Time Frame:

Variable, problem specific

Implementation:

Immediate when approved

Preservation Zone

These areas are remote and of sufficient size to ensure the long-term viability of wolves.

Objectives:

1. To maintain viable population of wolves in their natural state.
2. To provide opportunities for public access to unmanaged wolf populations.

Principles:

1. Wolves will not be killed in these zones
2. These zones will be established where land use compliments the strategy.
3. Ungulate hunting may be permitted in this zone, but will be a secondary use of the prey populations.

Implications:

1. Some prey populations may decline, or not continue to expand, eg. moose, elk.
2. The commercial/public use of wildlife will be impacted.
3. Wolves and their prey may stabilize at lower densities than managed populations.

Time Frame:

Permanent

Implementation:

After review process

Once the unresolved details of the strategy are finalized the plan will undergo public review. This review process will involve all groups interested in wolf management in B.C. This final strategy will provide the management framework for wolves in the province for the foreseeable future.

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APPENDIX

Symposium on Wolf-Prey Dynamics and Management

May 10 & 11, 1988

Room 166, MacMillan Building

University of British Columbia Campus

Vancouver, B.C., Canada

This technical wolf symposium is jointly sponsored by the Wildlife Branch of the British Columbia Government, Faculty of Forestry, U.B.C., and Northwest Wildlife Preservation Society.

Its purpose is to exchange information about wolf-prey interactions, covering both simple and multiple systems, as well as to deal with the issues of wolf management.

The first day addresses both single and multiple wolf-prey systems. The second day examines wolf management generally, and looks specifically at wolf management in British Columbia.

Registration is $10.00, payable to "B.C. Wolf Symposium." Advance registration is recommended as seating is limited to 150. Please send your fee along with the enclosed registration form to:

Dale Seip
Faculty of Forestry
U.B.C.
Vancouver, B.C. V6T 1W5

Tuesday, May 10

WOLF-PREY DYNAMICS

8:00 - 9:00	Registration
9:00 - 9:35	Predator-Prey Dynamics *-D. Seip*

Single Prey Systems:

9:35 - 10:10	Moose-Wolf Dynamics in Quebec *-F. Messier*
10:10-10:40	Coffee
10:40-11:15	Wolf-Deer Interactions on Vancouver Island *-D. Janz*
11:15-11:50	Moose-Wolf Dynamics on Isle Royale *-R. Page*
11:50-1:00	Lunch

Multiple Prey Systems:

1:00 - 1:35	Wolf-Moose-Caribou Interactions in Central B.C. *-D. Seip*
1:35 - 2:10	Wolf-Prey Interactions in the Yukon *-B. Hayes*
2:10 - 2:45	Wolf-Prey Interactions in Riding Mountain Park *-L. Carbyn*
2:45 - 3:15	Coffee
3:15 - 3:50	Wolf-Prey Interactions in Northeastern B.C. *-J. Elliott*
3:50 - 4:25	Wolf-Prey Interactions in Alaska *-W. Gasaway*
4:25 - 5:00	Questions
TBA	Reception

Wednesday, May 11

WOLF MANAGEMENT

9:00 - 9:25	IUCN/World Wildlife Fund Wolf Conservation *-M. Hummel*
9:25 - 9:50	Some Public Perspectives *-S. Pettigrew*
9:50 - 10:15	When is Wolf Control Justified? *-J. Theberge*
10:15- 10:45	Coffee
10:45- 11:00	Wolf Management in B.C. *-J. Walker*
11:00- 11:45	A Proposed Wolf Management Strategy *-R. Archibald*
11:45- 1:00	Lunch
1:00 - 2:30	Open Forum on Wolf Management

SPEAKERS

Ralph Archibald, B.C. Wildlife Branch
Lu Carbyn, Canadian Wildlife Service
John Elliott, B.C. Wildlife Branch
W. (Bill) Gasaway, Alaska Dept. of F. & G.
Bob Hayes, Yukon Game Branch
Monte Hummel, World Wildlife Fund
Doug Janz, B.C. Wildlife Branch
François Messier, University of Saskatoon
Rick Page, Michigan Technical University
Sherry Pettigrew, Northwest Wildlife Preservation Society
Dale Seip, University of British Columbia
John Theberge, University of Waterloo
Jim Walker, B.C. Wildlife Branch

Wildlife Working Reports should not be cited because of the preliminary nature of the data they contain

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WR-2 Progress report - year 2 - 1983, working plan - year 3 - 1984. Coastal grizzly research project. A.N. Hamilton and W.R. Archibald. First printed October 1984, revised October 1986. 32pp. (Also printed as WHR-10).

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WR-6 Kechika Enhancement Project of northeastern B.C.: wolf/ungulate management. 1983-84 annual report. J.P. Elliott. October 1984. 25pp.

WR-7 Muskwa Project working plan. J.P. Elliott. December 1984. 32pp.

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WR-18 Morice biophysical study, 93L/SW. B. Fuhr, M. Fenger, L. Lacelle, R. Marsh, and M. Rafiq. March 1986. 63pp + 9 maps.

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WR-24 Impacts of a hydro-electric reservoir on populations of caribou and grizzly bear in southern British Columbia. K. Simpson. February 1987. 40pp.

WR-25 The effects of snowmobiling on winter range use by mountain caribou. K. Simpson. February 1987. 15pp.

WR-26 Quesnel Highlands wolf control project. D. Hebert. January 1987. 10pp.

WR-27 Muskwa Wolf Management Project of northeastern B.C. 1986-87 annual report. J.P. Elliott. April 1987. 20pp.

WR-28 Vancouver Island wolf control project. Year 1 progress report. D. Janz. July 1987.

WR-29 Habitat survey of the Mackenzie Heritage Trail corridor. V. Hignett. June 1987. 21pp + 5 maps.

WR-30 A proposal to manage coyote and cougar populations of the Junction Wildlife Management Area. D. Hebert. September 1987. 11pp.

WR-31 Wildlife habitat suitability of the Mackenzie Heritage Trail corridor. V. Hignett. May 1988. 16pp + 6 maps.

WR-32 Research priorities for furbearers in British Columbia. D. Blood. June 1988. 49pp.

WR-33 Electrically triggered drop net to capture wild sheep. J.W. Hirsch. 1988. 18pp.

WR-34 A lynx management strategy for British Columbia. D.F. Hatler. July 1988. 121pp.

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